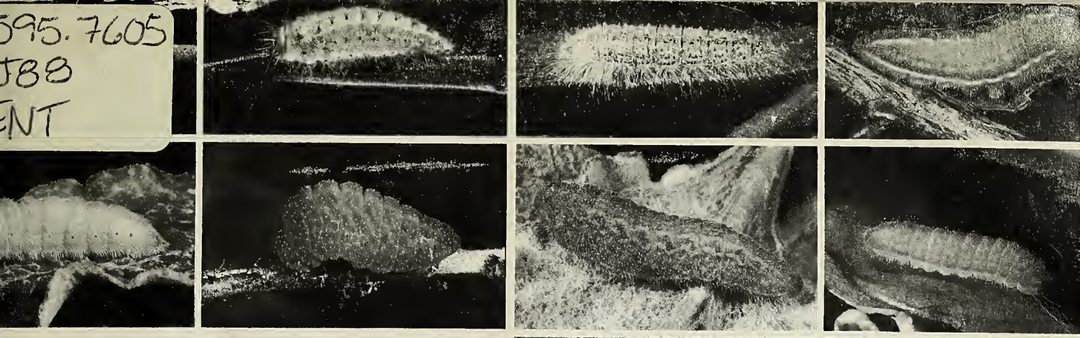

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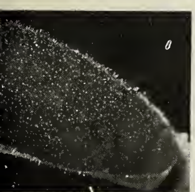

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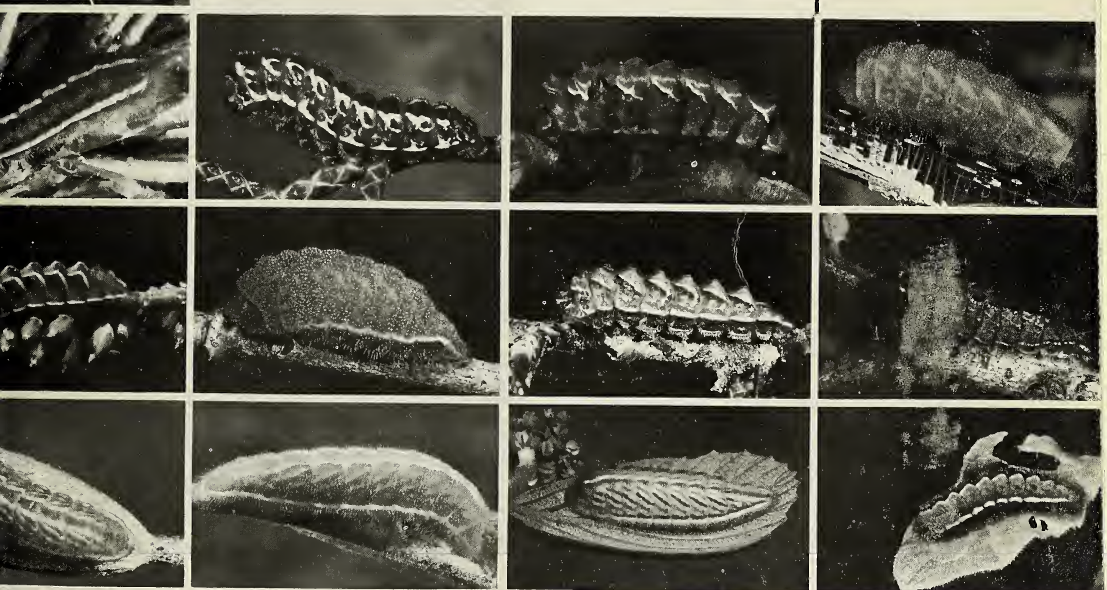

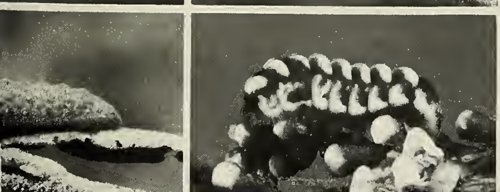

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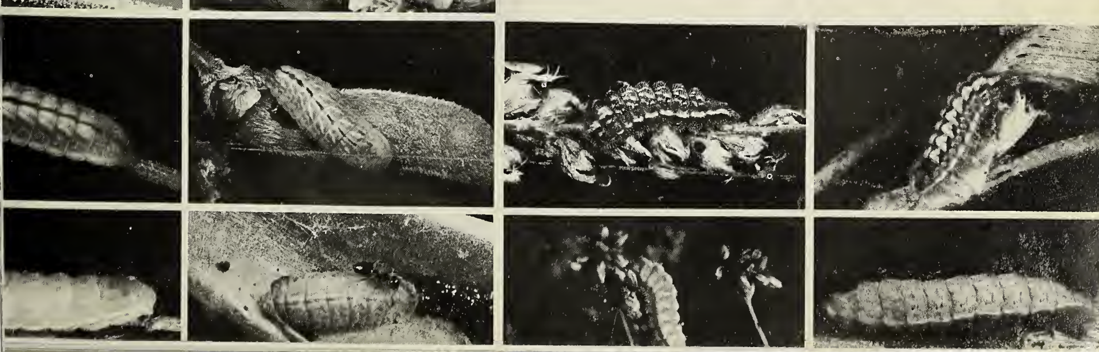

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A survey of the last instar larvae of the Lycaenidae (Lepidoptera) of California

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Abstract. The biology and last instar larval morphology of 69 species of California lycaenids are surveyed. Diagnostic descriptions of the subfamilies, genera, and species are provided together with a species key based primarily on larval morphology. Also included is a list of confirmed larval hosts including many host species not previously reported. Major aspects of the larval morphology of 29 exotic lycaenid species representing six subfamilies and 17 tribes are also reviewed for comparison.

Introduction

This is the first in a series of surveys of the mature larvae of the butterfly fauna of California. Included are 69 species of Lycaenidae which are listed in Appendix 1. Future works will survey the larvae of the Hesperiidae, Nymphalidae, Papilionidae, and Pieridae of California.

The Lycaenidae is perhaps the largest family of butterflies with nearly 40% of known butterfly species (Vane-Wright, 1978). The most recent comprehensive review of the group (based largely on adult characters) divides it into eight subfamilies excluding the Riodinidae (Eliot, 1973). Miller and Brown (1981) and Stehr (1987) also accord separate family status to the Riodinidae in spite of its placement as a subfamily of Lycaenidae by other authors (Ehrlich, 1958; Vane-Wright, 1978; Ackery, 1984; Scott, 1986). The classification of Eliot (1973) is retained here except that the Riodininae is considered subordinate to the Lycaenidae. Thus, the California lycaenids are divided into four subfamilies: Lycaeninae, Polyommatinae, Riodininae, and Theclinae. This arrangement is provisional and based largely on convenience, since most workers are familiar with these groups. Certainly these 'subfamilies' are not phylogenetically equivalent; a more precise hierarchic classification based on adult, larval, and biological characteristics awaits a broader faunistic survey beyond the scope of this work.

Although the life histories of nearly all species treated in this key have been published, most are inadequate for larval identification. The majority of larval descriptions have relied heavily on coloration with little attention to structural features. But color is perhaps the least reliable tool for identification since larvae of many species have similar coloration, some (especially polyphagous) species have multiple color morphs, and ground color may change in response to different food substrates (Orsak and Whitman, 1987). Also, larvae preserved in fluids often lose pigmentation; only melanic pigments associated with sclerotized structures such as the head, legs, and setae are resistant to fading.

Overall the most reliable characters for identifying larvae are structural. The presence, absence or condition of various organs and specialized setae are often diagnostic for higher taxa; the size, structure, and distribution of specific types of setae and other cuticular structures are often diagnostic for genera and species. Some species cannot be identified reliably by morphological traits but larval host, habitat, and locality data may provide additional clues to their identity.

Due to the paucity of detailed descriptions of larvae of the taxa treated in this work, a diagnostic description of each genus and a table of comparative characters for all species are included (Table 1). Some of the characters employed in these descriptions are new or poorly described in the literature and much of the terminology has not been standardized; therefore, a discussion of larval morphology and character terminology (with a glossary) is included. This discussion is not exhaustive but deals mostly with those characters found to be useful for identifying the species treated here.

Table 1. Comparative characters of california lycaenid larvae

Species	I.[1]	H.G.	E.T.	L.C.	M.S.	D.S.	H.W.	B.L.	N
Riodininae									
A. mormo	5	-	-	-	5	-	2.28	15	10
" *palmerii*	5	-	-	-	5	-	1.78	12	2
C. nemesis	5	-	-	+	4	-	1.45	16	9
" *wrighti*	5	-	-	+	4	-	1.60	14	6
Lycaeninae									
L. arota	4	-	-	+	2	-	1.61	17	10
" *cupreus*	4	-	-	+	2	-	1.26	17	8
" *editha*	4	-	-	+	3	+	1.67	18	10
" *gorgon*	4	-	-	+	2-3	-	1.74	18	10
" helloides	4	-	-	+	2	-	1.44	15	10
" *hermes*	4	-	-	+	2	-	1.31	15	5
" *heteronea*	4	-	-	+	2-3	+	1.63	18	10
" *mariposa*	4	-	-	+	2	-	1.53	15	3
" *nivalis*	4	-	-	+	2	-	1.42	20	10
" *phlaeas*	4-5	-	-	+	2	-	1.46	19	10
" *rubidus*	4	-	-	+	3	+	1.69	18	10
" *xanthoides*	4	-	-	+	3-5	+	1.87	24	10
Theclinae									
A. halesus	4	+	-	-	2	-	2.34	22	10
C. (C.) comstocki	4	+	-	-	2	+	1.17	15	9
" " *dumetorum*	4	+	-	-	2	+	1.42	19	10
" " *lemberti*	4	+	-	-	2	+	1.39	17	2
" " *perplexa*	4	+	-	-	2	+	1.33	15	10
" *(I.) augustus*	4	+	-	-	2	+	1.24	14	10
" " eryphon	4	+	-	-	2	+	1.75	17	9
" " *fotis*	4	+	-	-	2	+	1.16	16	10
" " *mossii*	4	+	-	-	2	+	1.40	18	10
". *(M.) johnsoni*	5	+	-	-	2	+	1.59	17	3
" " *loki*	5–7	+	-	-	2	-	1.62	16	10
" " *nelsoni*	5–7	+	-	-	2	-	1.55	15	10
" " *siva*	5–7	+	-	-	2	-	1.72	16	10
" " *spinetorum*	5	+	-	-	2	+	1.85	21	10
" " *thornei*	5–7	+	-	-	2	-	1.51	15	3
H. grunus	4	-	-	+	5	-	1.78	17	10
H. titus	4	+	-	-	6	+	2.02	24	4
M. leda	4	+	-	-	2	+	1.03	12	10
S. auretorum	4	+	-	-	3	+	1.56	18	10
" *behrii*	4	+	-	-	2	+	1.19	14	10
" *californica*	4	+	-	-	2	+	1.50	17	2
" *fuliginosum*	4	+	-	-	3	+	1.58	21	10
" *saepium*	4	+	-	-	2	+	1.44	17	10
" *sylvinus*	4	+	-	-	3	+	1.57	17	10
" *tetra*	4	+	-	-	3	+	1.78	19	10
S. avalona	4	+	-	-	2	+	1.15	13	6
" *columella*	4	+	-	-	2	+	1.11	14	10
" *melinus*	4	+	-	-	2	+	1.22	16	10
Polyommatinae									
A. franklinii	4	-	-	-	2	-	.86	13	3
B. exilis	4	+	+	-	2	-	.66	11	10
C. argiolus	4	+	+	-	2	+	.89	12	10

Table 1. con't

Species	I.[1]	H.G.	E.T.	L.C.	M.S.	D.S.	H.W.	B.L.	N
E. battoides	4	+	+	-	2	+	.63	9	10
" *enoptes*	4	+	+	-	2	+	.67	10	10
" *mojave*	4	+	+	-	2	+	.68	9	10
" *rita*	4	+	+	-	2	+	.60	10	10
E. amyntula	4	+	+	-	2	+	1.03	14	10
" *comyntas*	4	+	+	-	2	+	.83	12	4
G. lygdamus	4	+	+	-	2	+	1.11	19	10
" *piasus*	4	+	+	-	2	+	1.17	18	10
H. ceraunus	4	+	+	-	2	+	.73	12	10
" *isola*	4	+	+	-	2	-	.71	11	10
I. acmon	4	+	+	-	2	+	.77	11	10
" *icarioides*	4	+	+	-	2	+	1.03	17	10
" *lupini*	4	+	+	-	2	+	1.00	15	10
" *neurona*	4	+	+	-	2	+	.89	12	10
" *shasta*	4	+	+	-	2	+	.85	12	10
L. marina	4	+	+	-	2	+	.75	11	10
L. idas	4	+	+	-	2	+	.90	14	2
" *melissa*	4	+	+	-	2	+	1.00	16	10
P. sonorensis	4	+	+	-	2	+	1.10	17	10
P. speciosa	4	+	-	-	2	+	.65	10	10
P. saepiolus	4	+	+	-	2	+	.95	12	6
P. emigdionis	5-7	+	+	-	2	+	1.27	16	10

[1] I = larval instars; H.G. = honey gland; E.T. = eversible tubercles; L.C. = lateroseries of crochets; M.S. = mandibular setae; D.S. = dendritic setae; H.W. = mean head width (mm); B.L. = mean body length (mm); N = number of specimens measured for H.W. and B.L.; + = present, - = absent.

In order to understand better the distribution of morphological characters among higher taxa, larvae of several exotic species were also examined. Table 2 compares the following exotic species with respect to eight major morphological characters: Liphyrinae: *Liphyra brassolis* Westwood from Australia; Lycaeninae: *Heliophorus epicles* (Godart) from Malaysia; Miletinae: *Feniseca tarquinius* (Fabricius) from Illinois, *Spalgis epeus* (Westwood) from Thailand; Polyommatinae: *Anthene seltuttus affinis* (Waterhouse and Turner) and *Candalides xanthospilos* (Hübner) from Australia, *Everes argiades* (Palla) from Japan, *Erysichton lineata* (Murray), *Danis hymetus* (C. and R. Felder), *Lampides boeticus* (Linnaeus), *Syntarucus plinius* (Fabricius), a *Xylomelum*-feeding member of the *Theclinesthes miskini* (T.P. Lucas) — *onycha* (Hewitson) complex, and *Zizina labradus* (Godart) from Australia, and *Zizula hylax* (Fabricius) from Thailand; Riodininae: *Melanis pixe* (Boisduval) from Texas and *Zemeros flegyas* (Cramer) from Thailand; Theclinae: *Arhopala centaurus* (Fabricius) and *Cheritra freja* (Fabricius) from Thailand, *Deudorix epijarbas* (Moore) from Australia, *Erora quaderna* (Hewitson) from Arizona, *Eumaeus atala* (Poey) from Florida, *Flos areste* (Hewitson)

Table 2. Comparative larval features for some exotic lycaenidae

Species[1]	H.G.	E.T.	L.	S.L.	L.C.	M.S.	S.S.	Chalazae
Riodininae								
Hamearini								
Z. flegyas	-	-	+	+	+	2	+	simple
Riodinini								
M. pixe	-	-	+	+	+	24	+	simple
Liphyrinae								
L. brassolis	-	-	-	+	+	2	-	stellate
Lycaeninae								
H. epicles	-	-	+	+	+	4	+	simple
Miletinae								
F. tarquinius	-	-	+	+	-	2	-	simple
S. epeus	-	-	+	+	+	1	-	simple
Theclinae								
Arhopalini								
A. centaurus	+	+	+	+	+	5	+	buttressed
F. areste	+	+	+	+	+	6	+	buttressed
S. quercetorum	+	+	+	+	+	4	+	buttressed
Cheritrini								
C. freja	-	-	+	+	+	2	?	buttressed
Deudorigini								
D. epijarbas	+	-	+	+	-	3	+	buttressed
Eumaeini								
E. quaderna	-	-	+	+	-	2	+	stellate
E. atala	-	-	+	+	-	2	+	buttressed
Hypolycaenini								
H. erylus	+	-	+	+	+	2	+	buttressed
Luciini								
Hypochrysops sp.	+	+	+	+	+	4	+	simple
P. kamerungae	-	-	+	+	+	6	+	buttressed
Ogyrini								
O. genoveva	+	+	+	+	+	5	+	buttressed
Theclini								
H. crysalus	-	-	+	+	+	6	+	buttressed
Zesiini								
P. chlorinda	+	+	+	+	+	5	+	buttressed
Polyommatinae								
Candalidini								
C. xanthospilos	+	+	+	+	-	2	+	buttressed
Lycaenesthini								
A. seltuttus	+	+	+	+	-	2	+	simple
Polyommatini								
E. argiades	+	+	+	+	-	2	+	stellate
E. lineata	+	+	+	+	-	2	+	stellate
D. hymetus	+	-	+	+	-	2	+	stellate
L. boeticus	+	+	+	+	-	2	+	stellate
S. plinius	+	+	+	+	-	2	+	stellate
T. miskini-onycha	+	+	+	+	-	2	+	stellate
Z. labradus	+	+	+	+	-	2	+	stellate
Z. hylax	+	+	+	+	-	2	+	simple

[1] Complete citations in text; H.G. = honey gland; E.T. = eversible tubercles; L. = lenticles; S.L. = spatulate lobe on prolegs; L.C. = lateroseries of crochets; M.S. = mandibular setae; S.S. = sensory setae; + = present, - = absent, ? = presence or absence not determined.

from Malaysia, *Hypaurotis crysalus* (Edwards) from Arizona, *Hypochrysops apelles* (Fabricius) from Australia, *Hypolycaena erylus* (Godart) from Thailand, *Ogyris genoveva* Hewitson, *Philiris kamerungae* Waterhouse, and *Pseudalmenus chlorinda* (Blanchard) from Australia, and *Surendra quercetorum* (Moore) from Thailand.

The keys, diagnostic tables, and descriptions are based on observations by the authors of live and/or preserved larvae and photographs. Descriptions of genera and higher taxa are based on the California fauna except where noted. Distributional data has been compiled from several sources including publications and private collectors. Larval color descriptions are based on living material and/or color photographs.

Host plant information presented in the diagnostic section is based on published records and field observations by the authors; only relatively recent literature citations are given. Appendix 2 lists only those hosts confirmed by the authors' field collections; some reconfirm old records but many are new. The authors of botanical names are abbreviated according to the format of Munz and Keck (1959).

The majority of larvae examined were collected in the field by the authors or reared from ova from field collected adults. Larval morphology was determined primarily using a binocular dissecting microscope. The fine structures of some organs were further examined using a compound microscope with fiber-optic illumination and/or a scanning electron microscope (SEM). The orientation of line drawings and SEM photographs used for illustration are standardized (unless otherwise indicated) with cephalad to the left (lateral views) or top (dorsal views).

The key and descriptions apply to last instar larvae. Although the number of larval instars in some Lepidoptera may depend upon environmental variables and diet, most California lycaenids appear to have a constant number of instars. Most species have four instars but the riodinines, one polyommatine, and six theclines typically have five or more instars. In the Lycaenidae the last instar often differs morphologically from previous instars. Since the instar in which various organs and specialized setae first appear varies for different taxa, the best general means of determining the instar is larval size. Although body length increases within an instar, sclerotized body regions such as the head remain constant in size between molts.

The head width for last instar larvae of each species is included in Table 1 along with the body length (from anterior margin of the prothorax, excluding the neck, to the caudal margin of abdominal segment 10) to aid in determining larval instar and to indicate comparative size among species. All measurements are in millimeters and are based on preserved larvae. For most species these values are derived from a single collection or pooled collections of ten individuals representing a single population. Different preservation methods, as well as larval condition at the time of preservation, can result in different body length and width dimensions. The problem of morphological variability

among subspecies is discussed for a few species where it may aid in identification. A broader discussion of all subspecies is beyond the scope of this work.

The most effective use of the key requires a binocular dissecting microscope since major emphasis is placed on small morphological features. Whenever possible one should attempt to identify larvae while they are alive because some structures are best seen while the larval surface is dry and because coloration may be useful.

There are several effective techniques for larval preservation; the most important considerations are to distend the larva and fix the tissues. Commonly larvae are killed in KAAD (kerosene, ethanol, acetic acid, and dioxane) or other fluids which both distend and fix them. Another satisfactory method is to inject the larva through the anal opening with a fixative such as Kahle's fluid until it is sufficiently distended and/or fix it in hot water (70-85 degrees C.) for about five minutes. Larvae are usually stored in 70-80% ethanol; they should not be put into alcohol until they have been properly fixed. Inflated, freeze-dried, and critical point-dried larvae are also satisfactory for identification but may be difficult to store and handle. Dry or shriveled larvae, larval exuviae, and carcasses remaining after parasite emergence may be identifiable after softening in 5% potassium hydroxide solution. For a broader discussion of methods for larval preservation see Peterson (1948) or Stehr (1987).

LARVAL MORPHOLOGY

The immature stages of many species of Lycaenidae are commonly associated with ants. This association is reflected in the specialized morphology of the larvae among which a variety of myrmecophilous adaptations have evolved (see Hinton, 1951; Henning, 1983b; Cottrell, 1984; Kitching and Luke, 1985).

The known mature larvae of most lycaenids (including nearly all California species) share a few morphological features which (in combination) distinguish them from all other Lepidoptera. The presence of cuticular lenticles and a fleshy terminal lobe on the prolegs are almost unique to this family where they occur in most known species. Other distinctive features such as an onisciform body shape, retractable head, eversible tubercles, and honey gland are somewhat less widely distributed in the Lycaenidae. The full extent of the distribution of these and other diagnostic features remains speculative since the larvae of most species remain undescribed. Generalizations are further hindered by the morphological diversity encompassed by those species which have been investigated.

A clearer understanding of the relationships among higher taxa in the Lycaenidae can probably by gained by broad faunal surveys of their immature stages as suggested by Henning (1983a), Cottrell (1984), and De Vries et al (1986), yet few such works exist. Malicky (1969a, 1969b, 1970) surveyed the larval morphology (especially ant-associated organs) of Central European lycaenids and produced a key based on their morphology, coloration, and host plants. Scott (1986) produced a last instar larval key to the families, subfamilies, and some tribes of North American butterflies; his key is more detailed than those of Peterson (1948) and Stehr (1987), which pertain to all North American Lepidoptera, but fails to consider the full range of diversity in North American lycaenids.

The shape of lycaenid larvae is often termed onisciform (shaped like a sowbug or woodlouse, *Oniscus*). The prothorax (T1) is often the longest segment since in most species the head is retractable into it. The body is usually broadest and highest at the mesothorax (T2), metathorax (T3), or first abdominal segment (A1) and gradually tapered posteriorly. Abdominal segments ten (A10), nine (A9), and (usually to a much lesser extent) eight (A8) are fused to varying degrees in different groups. In cross-section the body is typically convex dorsally and flattened ventrally. The dorsum may be evenly rounded but in some species paired dorsal prominences (flanking the middorsal line) create a trapezoidal outline in cross-section and a saw-toothed lateral profile. Middorsal prominences occur in some exotic species such as *Cheritra freja* of southeast Asia. The junction of the lateral and ventral body regions typically forms a fleshy lateral fold (often fringed with long setae) which conceals the legs when at rest. When inflated (as commonly occurs during preservation) the body may assume a more cylindric shape

typical of other Lepidoptera. An onisciform body is typical of the subfamilies Curetinae, Liphyrinae, Lycaeninae, Polyommatinae and Theclinae; but the larvae of some Miletinae and many Riodininae are much less onisciform while those of the exotic Lipteninae and Poritiinae are not at all (Cottrell, 1984).

The lycaenid larval head is commonly much narrower than the thoracic segments and attached to a neck-like extension of the prothorax into which it can be withdrawn. The size of the head relative to body width, the neck length, and degree to which the head can be withdrawn are variable among (and to a lesser degree within) the lycaenid subfamilies. Among the California fauna the head is smallest and neck generally longest in the Polyommatinae while the head is largest and neck shortest in the Riodininae. A broad nonretractable head is typical of the known larvae of Riodininae and of some other subfamilies such as the Miletinae (including *Feniseca tarquinius* of eastern North America) and of the Florida thecline *Eumaeus atala*.

Other morophological features common to mature lycaenid larvae include the presence of prolegs on A3-A6 and A10 (anal prolegs) and numerous secondary setae. Also, with few exceptions the crochets on the prolegs are arranged in a mesoseries divided by a fleshy lobe (fig. 72); some species also have a lateroseries of crochets (fig. 72a). Most known lycaenids, including all California species, possess a well defined prothoracic shield (fig. 1). A well developed (sclerotized) suranal shield is present in many exotic species but not in California lycaenids; a poorly developed suranal shield is present in the riodinines and in *H. grunus*.

Many lycaenids in the Curetinae, Liphyrinae, Polyommatinae, and Theclinae possess a pair of eversible tubercles on the eighth abdominal segment (fig. 1, 20) and/or a honey gland (Newcomer's organ) usually located on the seventh abdominal segment (figs. 1, 19). In the Southeast Asian thecline, *H. erylus*, the honey gland is located on the eighth abdominal segment. Analogous structures are present in some exotic riodinines such as *Anatole rossi* Clench which has paired eversible tubercles on the metathorax and paired eversible honey glands on the eighth abdominal segment (Ross, 1964). Honey glands produce a fluid which ants imbibe while the eversible tubercles may either attract or excite ants by releasing semiochemicals which mimic the ants' own pheromone(s) (Henning, 1983a and b). Cuticular lenticles, which probably occur in most lycaenids (see lenticle discussion below), apparently also have a chemical communication function (Malicky, 1970; Henning, 1983a and b).

A few characters permit an easy distinction between the larvae of riodinines and other lycaenids in California. Among the riodinine larvae the longest setae are clustered in tufts or verrucae (figs. 30, 31, 69, 70) and are frequently longer than the head width; the prothoracic shield is transverse (the length along the dorsal midline is about half as

great as the width) and adorned with several conspicuously long setae which extend anteriorly over the head (fig. 5). Perhaps the best distinguishing feature of the riodinine larvae is the anteroventral displacement of the A1 spiracles to a location just anterior and slightly ventral to the lateral verrucae (figs. 30, 69, 70) where they may be concealed by a cuticular fold; spiracles on the other abdominal segments are located about midway between the dorsal and lateral verrucae. This condition probably applies to most New World riodinines (Don Harvey, 1987 and *in litt.*), but not to the Old World taxa. Among the larvae of other California lycaenids all setae are shorter than the head width and randomly scattered over the body; the prothoracic shield is often approximately diamond-shaped (figs. 33-54, 61, 64, 67, 71) and is usually as long or longer than wide; no setae on the shield extend forward as far as the anterior margin of the prothorax (fig. 1).

Some exotic riodinines possess additional features which apparently do not occur in other Lepidoptera families. For example, the neotropical species *A. rossi* (Clench), *Audre epulus signatus* (Stichel), and *A. susanae* (Orfila) have a pair of vibratory papillae on the prothorax and paired honey glands on the eighth abdominal segment (Ross, 1964; Bruch, 1926; and Bourquin, 1953, respectively). Larvae of *A. rossi* also possess a pair of eversible tubercles on the metathorax (Ross, 1964). The aforementioned species are notably myrmecophilic, unlike the California riodinines.

Chaetotaxy is the primary tool for identifying most Lepidoptera larvae yet detailed systematic descriptions of lycaenid larval chaetotaxy are uncommon. Clark and Dickson (1956b) proposed the use of first instar setal patterns as a tool for elucidating phyletic relationships in the Lycaenidae and later (1971) described the early stages of the South African fauna. Other workers (Lawrence and Downey, 1966; Downey and Allyn, 1979 and 1984; and Wright, 1983) provided detailed descriptions of four North American species. In each of the latter works a modified version of Hinton's (1946) setal nomenclature was employed to describe (primarily) the first instar chaetotaxy. These authors also recognized a variety of structural forms of setae, some of which were found only in later instars.

Hinton (1946) recognized two functional types of setae in the order Lepidoptera: **microscopic** or proprioreceptor setae located along intersegmental folds and where different body parts make contact, and long or **tactile** setae which are more widely distributed and may be modified for specialized functions. The microscopic setae have received little attention by investigators due to their small size while the structure and distribution of tactile setae are widely employed in identifying larvae of many families of Lepidoptera.

Tactile setae may be further categorized as **primary, subprimary,** and **secondary.** Primary setae, found in specific body locations, are believed to represent the archetypal lepidopteran setal pattern and, with few

exceptions, are discernible at least in the first instar. Subprimary setae, always few in number, also occur in fixed locations which are characteristic of some families. In most groups where they occur subprimary setae appear in later instars but in highly specialized families such as the Lycaenidae they occur in the first instar. Secondary setae, which are numerous in some families, are variable in number and position, generally most abundant in the last instar, and only rarely occur in first instars.

For most (perhaps all) lycaenids the distribution pattern of primary and subprimary setae is obscured by numerous secondary setae in instars following the first. Among the fauna included in this survey there are several structurally distinct types of secondary setae whose size, number, and distribution are often taxonomically useful.

The basic setal structure consists of a hollow shaft (usually with lateral processes or spiculations) arising from a basal ring which surmounts a short sclerotized prominence or chalaza. In the Lycaenidae variations in setal structure range from long, slender, and finely tapered to short, stout, and capitate while their lateral processes range from long slender filaments to short, stout, pointed dentations and minute granulations. In some taxa setal structure is nearly uniform regardless of setal size or location but more often the longest setae are most erect and most tapered while the shortest setae are most curved and/or clavate. The longest setae also tend to be in locations where true primary setae are expected to occur (i.e. dorsal, subdorsal, lateral, etc.). Often there is a gradient in setal structure with the most clavate, capitate, or recurved setae occurring dorsally on A7-A10. Setae with the longest lateral processes (relative to setal length) occur most frequently in close proximity to the honey gland and spiracles.

In the known larvae of New World riodinines most setae are gradually tapered, filamentous, or short and multibranched while strongly bent setae are absent or rare. Also, the longest setae (often much longer than the head width) arise from the prothoracic shield and/or dorsal and laterval verrucae. But in the Old World *Z. flegyas* setal structure is often more complex and those setae on the prothoracic shield barely reach the posterior cranial margin. In *Calephelis* the longest setae may be longer than the body width while the shortest setae, which occur densely over the dorsal and lateral regions, are too small to be individually discerned without magnification. In *Apodemia* all body setae are gradually tapered or filamentous and those arising from verrucae are primarily stiff and spinelike.

For the purpose of describing the larvae treated in this survey seven common categories of setae are defined: 1) **prominent** (figs. 2a, 4), 2) **dendritic** (figs. 2p, 15-18), 3) **sensory** (figs. 6, 9-14), 4) **neck** (fig. 27), 5) **mushroom** (figs. 2q, 22), 6) **plumose** (figs. 31, 32), and 7) **echinoid** (fig. 31). Prominent and sensory setae occur in all lycaenid subfamilies represented in California but dendritic and neck satae are absent in the

Riodininae, mushroom setae occur only in the Lycaeninae, and plumose and echinoid setae occur only in the Riodininae. The first four setal categories are widespread in the Lycaenidae; the last three may occur only in relatively small groups (subfamily, tribe, etc.) and it is likely that other structurally equivalent setal categories could be defined for other small phyletic groups. However, the majority of larval setae do not fit the categories enumerated above; they comprise an unnamed assemblage of perhaps less specialized setae with diverse structures (figs. 2b-2o).

Prominent setae of Lycaenidae occur in specific locations which coincide with sites where true primary setae are found in most other Lepidoptera. However, the number of prominent setae in a given location is variable and often exceeds the basic number of primary setae; they may also be absent. They are always cylindric, tapered, erect, and straight to gently curved (figs. 2a, 4); in many species they differ from surrounding setae only in their much greater length. This setal category corresponds to the major setae of Lawrence and Downey (1966), Downey and Allyn (1979), and Wright (1983). Prominent setae on the prothorax usually occur abundantly along the anterior and lateral margins where they can serve as the anterior most tactile receptors when the head is withdrawn. Additional prominent setae may occur on the prothoracic shield or near its anterior and posterolateral margins. On all other segments prominent setae occur singly or in groups dorsally (flanking the middorsal line), subdorsally (about half way between the spiracles and middorsal line), and laterally (below the spiracles, along the lateral fold) (fig. 1). Aside from the prothorax, prominent setae tend to be most abundant on the mesothorax and progressively less abundant posteriorly, although there is usually little difference in their numbers on A1-A6. In species having a honey gland there are no dorsal prominent setae on A7. Subdorsal prominent setae are least encountered but usually occur on T2 and are more likely to occur on A6 and A7 than on A1-A5. Lateral prominent setae usually occur on all segments but are reduced or lacking in some species. Prominent setae are almost always present along the anterior and lateral margins of the prothorax and posterolaterally on A10. In the California riodinines most prominent setae occur on verrucae and the prothoracic shield. In *Apodemia* they are primarily stiff and spinelike but in *Calephelis* they are mostly long, slender, and plumose. These latter setae are morphologically distinctive enough to be accorded a separate setal category (plumose setae) discussed below.

Dendritic setae can be distinguished from other secondary setae by structure and location. They may appear tree-like due to the presence of filamentous lateral processes arising from the apical half which are usually longer than the setal width at their point of origin. These setae are weakly tapered to clavate, erect, straight (rarely slightly curved), and less pigmented than other setae. They are usually restricted to a few

locations (where lenticles may also be concentrated) such as the margin of the honey gland and spiracles, but are more widespread in some taxa and absent in others. Commonly at least a pair of dendritic setae occurs at each lateral angle of the honey gland where they may be obscured if the gland opening is retracted. The dendritic appearance of these setae varies due to the relative length of their lateral processes. Although the processes are usually much longer than the setal width (figs. 15-17), they can be shorter and may not be easily seen (especially those at the lateral angles of the honey gland) (fig. 18). In such cases dendritic setae can usually be distinguished by their greater prominence (surrounding nondendritic setae are often shorter and clavate-capitate or recurved). Lawrence and Downey (1966) used the terms spiculate and dendritic for this type of setae on the larva of *E. comyntas* and likened their appearance to Christmas trees. Other terms for dendritic setae which appear in the literature include spiculate and hydroid setae (Downey and Allyn, 1979) and branched hairs (Kitching, 1983).

The function of dendritic setae is not well established but there are indications that they may be involved in chemical and/or tactile communication with ants. Our observations indicate a direct relationship between the abundance of these setae and the degree of ant-larval association (research in progress). Thus, while larvae of all twelve California species of Lycaeninae lack the more notable ant association organs (honey gland and eversible tubercles), the four which have dendritic setae are the only ones which we have found associated with ants.

Although all setae may have a sensory function, the term sensory setae has been applied to a unique pair of setae on the lycaenid prothoracic shield (Downey and Allyn, 1979 and 1984). They have also been termed XD2 (*op. cit.* and Wright, 1983) and major setae 'type a' (Lawrence and Downey, 1966). But setae of homologous structure found in other Papilionoidea and at least some Arctiidae, Geometridae, Saturniidae, and Sphingidae occur anterior and/or anterodorsal to the T1 spiracles and often subdorsally on other segments; their location coincides with Hinton's SD1 setae. These are the only primary body setae which can be recognized in all lycaenid instars. They occur in all California lycaenids and in nearly all exotic species examined; none were found in the liphyrine *L. brassolis* nor in the miletines *F. tarquinius* and *S. epeus*. The function of the sensory setae is unknown and they are curiously insensitive to tactile stimulation.

The structure of the sensory setae varies among different taxa. They may be filiform, flagelliform (fig. 14), clavate (fig. 12), spatulate (fig. 13), or even branched (fig. 6). In most species the sensory setae have inconspicuous lateral spicules but in others the spicules are longer, causing the sensory setae to appear brush-like (fig. 9). In the Lycaeninae the lateral spicules are confined to the apex (best seen with SEM) or absent (fig. 14). Sensory setae are more slender, at least basally, often

longer, and more flexible than other setae on the prothoracic shield; they arise from uniquely low, button-like chalazae. In live larvae their flexibility and fine basal attachment result in a vibratory or slow twitching motion in weak air currents which may cause them to appear independently motile.

Mushroom setae are known to occur only in members of the Lycaeninae (Wright, 1983). Malicky (1969) referred to this type of seta as Baumchenhaare (tree setae) in his treatment of the European *Lycaena* species. Under low magnification they appear as short, rounded structures resembling mushrooms but with higher magnification they can be seen to have numerous short, stout distal and lateral processes (figs. 2q, 22). They are usually nonpigmented and much shorter than other setae among which they are scattered over the dorsal and lateral body surfaces. To the unaided eye they may appear as minute white speckles in contrast to the darker larval ground color. Structural variations in the mushroom setae, especially their lateral processes, may be useful taxonomic characters (figs. 2q and 22) but since these cannot be seen without SEM they are of little use in larval identification.

The lycaenid larval neck can be densely covered with minute setae and/or spinules which give it a granular appearance. These neck setae typically are much shorter than other secondary setae, stout (often tooth-like), may be rounded or acute apically, and may have a few short, stout apical or subapical spicules (fig. 27). Spinules are shorter than neck setae and range from pointed to rounded and may be erect or recumbent (figs. 27, 28). Both neck setae and spinules are apparent on the posterior half of the neck where their distribution usually ends abruptly at the junction with the nonretractable remainder of the prothorax. In some lycaenines and theclines neck setae are also sparsely scattered dorsally and laterally over the remainder of the prothorax. Under the dissecting microscope it may be difficult to discern whether they are setae (with supporting chalazae) or merely spinules. In the Theclinae and Lycaeninae both neck setae and spinules are abundant on the posterior half of the neck. In the Polyommatinae there is a narrow dorsal band of spinules at the posterior end of the neck and a more extensive ventral patch of spinules and neck setae anterior to the prothoracic legs. Neck setae and spinules were not observed in the Liphyrinae, Miletinae, and Riodininae. Although differences in the structures of the neck setae and spinules may provide characters for taxonomic studies they are difficult to observe without SEM and are not discussed further here.

Plumose setae occur only in the riodinines and are most apparent on the prothoracic shield and verrucae. They are slender filaments densely clothed with short, fine lateral processes which may confer a velvety appearance (figs. 31, 32). These setae are mostly uniform in width throughout most of their length but may be apically spatulate (fig. 32) or abruptly tapered. In *A. mormo* a single plumose seta may arise from

each dorsal verruca and 4 or more from each lateral verruca along with numerous shorter spine-like setae (fig. 69), but in *Calephelis* the verrucae are comprised entirely of plumose setae (fig. 70). In the latter genus these setae vary greatly in length but many are longer than the body width and confer to a larva the appearance of a down feather; much shorter plumose setae occur primarily near the verrucae, on the prothoracic shield, and near the intersegmental lines. Also in *Calephelis* a few plumose setae on dorsal verrucae are relatively short, stout, and somewhat spatulate.

Echinoid setae were found only in *Calephelis* larvae. Due to their small size and density they may cause the body surface to appear pollinose or mealy. They are rather short and stout and adorned with relatively large lateral processes which taper from broad bases but are apically flared (fig. 31). Other authors have referred to these setae as many-pointed branching stars in *C. wrighti* (Comstock, 1928), stellate nodules in *C. nemesis* (Comstock and Dammers, 1932), silvery stars in *C. borealis* (Grote and Robinson) (Dos Passos, 1936), and sprocket-shaped processes in *C. muticum* McAlpine (McAlpine, 1938).

Other secondary setae span a wide range of structural forms including erect, recumbent, straight, recurved, tapered, and clavate-capitate (figs. 2b-2o). In some species these setae are uniform in structure but commonly there is a structural gradient with the most extreme forms occurring in specific areas. The most recurved and clavate or capitate setae usually occur dorsally on abdominal segments 7-10 (especially near the honey gland). The nearly continuous range of structural variation in these setae among different species and even on individual larvae diminishes the value of defining specific structural types for them.

All setae on the larval body normally arise from sclerotized tubercles or **chalazae**. Ventral chalazae are typically cylindric but dorsal and lateral chalazae may be sculptured in the Polyommatinae and Theclinae. The chalazae of most species of Polyommatinae appear stellate or crown-like due to conspicuous lateral or distolateral points (figs. 2e, 2f, 2j, 2k, 13, 16). In the Theclinae the chalazae are most often conical with longitudinal ridges resembling buttresses which are most prominent basally where they fuse with the cuticle (figs. 2n, 2o, 4); similar chalazae occur in the Curetinae (DeVries, et al, 1986). In the liphyrine *L. brassolis* the dorsum is covered with highly modified flattened, shingled chalazae bearing much smaller setae; toward the ventral margin of the dorsal carapace these chalazae become more erect and cylindric and appear somewhat stellate. In all Lycaeninae, Miletinae, and Riodininae examined the chalazae are smoothly contoured and cylindric or globular (figs. 2i, 15). Although the structural distinctions between the chalazae of the Polyommatinae and Theclinae are true for most species examined, there are some exceptions. In the polyommatines *P. emigdionis* from California and *C. xanthospilos* from Australia, the chalazae appear

buttressed rather than stellate. In the former species SEM photographs show that the lateral ridges are not distobasally fused with the cuticular surface (fig. 10) but in the latter they are very similar to typical thecline chalazae. Larvae of the Arizona thecline, *Erora quaderna*, have stellate chalazae much like those of the Polyommatinae. Also, some members of both subfamilies have apparently nonsculptured chalazae as in the Lycaeninae.

In many lycaenids the degree of sculpturing of the chalazae varies for different types of setae and in different body regions. The most sculptured and strongly pigmented chalazae often occur on or near the prothoracic shield. Chalazae associated with dendritic setae are usually less sculptured than those of other setae and may appear nonsculptured. In the Polyommatinae the chalazae of prominent setae tend to be larger but less stellate than those of shorter adjacent setae. The chalazae associated with neck setae and the sensory setae on the prothoracic shield are not sculptured. The latter are visibly low and button-like (figs. 6, 9, 11, 12, 14) in the Lycaeninae, Theclinae, and Riodininae whereas in the Polyommatinae they are often slightly sunken below the cuticular surface (figs. 10, 13). Their visible dorsal surface is glassy smooth and flat or convex, much like a lenticle with a small central pore from which the sensory seta emerges.

Lenticles are small lens-like cuticular structures often resembling chalazae without setae; they may be present in all lycaenids and thus constitute an important diagnostic character. Other terms for lenticles include perforated cupolas (Malicky, 1970), Allyn's organs (Downey and Allyn, 1979), and pore cupolas (Kitching and Luke, 1985). Malicky (1970) found them in 60 species of (primarily European) lycaenids. In this study they were found in all lycaenid species examined except *L. brassolis*. The larval dorsum in that aberrant species is densely covered with overlapping chalazae; but there are regularly placed pores which may lead to recessed glands and/or lenticles, as suggested by observations of the inner surface of larval exuviae (Bethune-Baker, 1925).

Lenticles have a low, round, convex or flat central region surrounded by a narrow collar; the latter may be smoothly rounded and cylindric, buttressed, or stellate much like the chalazae of nearby setae (figs. 15, 16, 17, 19). Although the lenticles of first instar larvae are few in number and occur in fixed locations, those of later instars are more numerous, variable in number, and more randomly distributed. In mature larvae lenticles tend to be sparsely scattered over dorsal and lateral body regions but more numerous near the honey gland and spiracles (especially on A8).

The function(s) of the lenticles remains somewhat speculative but at least some seem to be related to myrmecophily. Malicky (1970) suggested that lenticles have a chemical communication function since they are most abundant in areas commonly attended by ants and at least some have a porous surface and are associated with epidermal glands.

Lenticles of similar structure occur in hesperiid larvae (which are not myrmecophilous) where they have been shown to be formed by cells which can also produce setae (Franzl et al, 1984). Henning (1983b) found in some South African lycaenids that the body surface containing lenticles also contains a chemical which mimics an associated ant's brood pheromone.

A specialized type of lenticle, found in *A. halesus*, has a mushroom shape. **Mushroom lenticles** differ from other lenticles primarily in being stalked or elevated above the body surface and narrowest at the base; also, the collar surrounding the central lens is relatively broad and divided into radial segments by narrow ridges (figs. 6, 26). Under low magnification these lenticles appear similar in size and form to the mushroom setae of *Lycaena* larvae and, likewise, confer a minutely white speckled appearance to the larva. They are randomly distributed over the dorsal and lateral body regions but replaced by more ordinary appearing lenticles on the prothoracic shield and areas adjacent to the spiracles and honey gland.

The presence of a pair of **eversible tubercles** (tentacular organs) dorsolaterally on abdominal segment eight is a common trait in the Lycaenidae; they have been reported in the subfamilies Curetinae, Liphyrinae, Polyommatinae, and Theclinae (Cottrell, 1984). The appearance of these organs differs little among the California species. Ordinarily they are retracted into the body but when everted they can be seen (in most species) to have an apical cluster of relatively long, straight, prominently spiculate setae (fig. 20). The spicules on these setae are slender and rather evenly distributed whereas those of dendritic setae, which they otherwise resemble, are concentrated in the apical half of the seta. In some exotic taxa variations in the structure of the tubercles and in the number, size, and color of their terminal setae are of taxonomic value (Clark and Dickson, 1956a); the eversible tubercles of some exotic species such as *Ogyris genoveva* and *Candalides xanthospilos* lack setae.

Among the California fauna eversible tubercles are absent in the Lycaeninae, Riodininae, and Theclinae but well developed in all Polyommatinae except *A. franklinii* and *P. speciosa*; they may be nonfunctional in some populations of *E. amyntula*. Generally these organs are everted briefly at irregular intervals or in response to tactile stimuli but in some, such as *P. emigdionis*, they pulsate regularly and are frequently everted as the larva crawls. The function of the tubercles may vary among different taxa; Clark and Dickson (1956a) felt that 'whip' type eversible tubercles in Aphnaeini mechanically remove bothersome ants; some other authors (Henning, 1983a and b; De Vries, 1984; Kitching and Luke, 1985) suggest that the tubercles in other taxa release a chemical which mimics an ant alarm pheromone. In preserved larvae they are seldom everted, but their locations usually can be discerned by the presence of a small circle of setae surrounding a bare

wrinkled depression (which may surmount a low prominence) slightly posterolateral to the eighth abdominal spiracles.

The **honey gland** (Newcomer's organ or dorsal nectary organ) is a feature present in many species of Polyommatinae and Theclinae but apparently absent from other lycaenid subfamilies. It usually appears as a narrow transverse middorsal furrow on A7; in the exotic *H. erylus* the honey gland occurs on the eighth abdominal segment, closely flanked by the spiracles. In response to stimulation by ants the gland can partly evert (fig. 19) and discharge a drop of fluid which ants imbibe. For some species this fluid has been shown to contain both sugars and amino acids (Maschwitz et al, 1975; Pierce, 1983). In discussing the relationship between ants and lycaenid larvae, Malicky (1969, 1970) suggested that the honey gland provides a bribe to forestall aggression by ants. Pierce and Mead (1981) noted that ant-tended larvae of *G. lygdamus* were significantly less parasitized than untended larvae and suggested that the honey gland attracts ants which defend the larva much as they do other nectar sources. Henning (1983b) minimized the importance of the honey gland and suggested that chemicals produced by other organs (chiefly lenticles) were responsible for maintaining a benign (even protective) attitude by ants toward lycaenid larvae. A honey gland is not necessary for attracting ants since mymecophily occurs in some taxa, such as *Lycaena*, which have no honey gland. Among California lycaenids the honey gland is absent in the Lycaeninae and Riodininae, but present in all Polyommatinae except *A. franklinii* and in all Theclinae except *H. grunus*. The external gland opening is usually surrounded by numerous lenticles and often by dendritic setae as well. In some exotic species the base of the gland and/or the surrounding cuticle is strongly sclerotized, but in the local fauna little or no sclerotization is apparent. Although the surrounding setae may provide useful diagnostic characters, the appearance of the honey gland itself is of little use in discriminating the local fauna.

The arrangement of the **crochets** and presence of a **spatulate lobe** on the prolegs are good characters for distinguishing most lycaenids. Typically in this family there is a well developed bi- or triordinal mesoseries of crochets which may be weakened or divided medially by a fleshy lobe (fig. 72). Many taxa also have a less well developed lateral series of crochets; in *L. brassolis* it is so well developed that an essentially complete ring of crochets is apparent. In the California fauna a lateroseries of crochets occurs in the Riodininae (except *A. mormo*), in the Lycaeninae (sometimes greatly reduced or absent on some prolegs) and in *H. grunus* (fig. 72a). The fleshy lobe which often divides the mesoseries of crochets is strongly spatulate in most species but absent in both *A. mormo* and *P. emigdionis*.

Cephalic pigmentation is a useful diagnostic character for several taxa. In most California Polyommatinae the cranium is uniformly dark brown or blackish but in the Lycaeninae and Theclinae it is often

yellowish. The cranium is usually dark in *A. mormo* but pale or nonpigmented in the other three riodinine species. A narrow band of dark pigment is usually associated with ocelli (stemmata) 1-5 (fig. 45); ocelli are numbered as in fig. 68. One should not confuse this cuticular infuscation with the subcuticular ocellar pigment which is often visible in preserved specimens. A few local and many exotic polyommatine species have light brown head color while some lycaenine and thecline species have extensive dark cranial infuscation.

Cephalic setation is a relatively conservative trait in most lycaenid groups. Cranial setae are usually few in number and very small (fig. 3) except for those near the oral margin. More numerous short setae (similar to neck setae) may occur, especially in the Lycaeninae and Theclinae, on the frons (fig. 29) and ventral to the ocelli. The cranial secondary setae of the Riodininae are more numerous and may be as long as some prominent setae on the body (fig. 5).

The number of **mandibular setae** may be variable but is useful in distinguishing some taxonomic groups. This character was examined for only a limited number of specimens of each species. Although it has been reported that riodinines have more than two mandibular setae while other lycaenids have only two (Scott, 1986; Downey, 1987; Harvey, 1987), there are numerous exceptions. In this study two mandibular setae were found in all polyommatines, most theclines (fig. 55a), and in the Southeast Asian riodinine, *Z. flegyas*. But some theclines have as many as six mandibular setae, while two to five were found in the Lycaeninae (fig. 55b); 24 mandibular setae were found in the riodinine *M. pixe*. *Spalgis epeus* has one madibular seta.

There are notable differences in the **prothoracic shield** among the California taxa surveyed here. In the riodinines the shield is transverse, rather strongly sclerotized, and adorned with numerous long setae which overhang the head. In the other lycaenids the shield is about as long as it is wide (sometimes longer), variably sclerotized, somewhat recessed below the level of the surrounding cuticle (figs. 1, 21), and has setae which seldom extend much beyond its anterior margin. In the Lycaeninae, Riodininae, and Theclinae the surface of the prothoracic shield usually appears smooth (figs. 9, 11, 12, 14, 21). In polyommatines the surface of the shield appears (in SEMs) honeycombed with a complex ultrastructure of anastomozing ridges similar to, but more highly developed than, those elsewhere on the body (figs. 10, 13); this surface also occurs on the prothoracic shield of some theclinae such as *A. halesus* (fig. 6).

Body coloration is highly variable in the Lycaenidae since most species are cryptically colored to match their substrate. The predominant ground color is green but pink, white, yellow, and brown are also common. Except in the riodininae a disruptive pattern of contrasting lines is often present. The latter may appear complex but usually can be reduced to a few standard components.

The following color pattern components are recognized: 1) **middorsal line**, 2) **subdorsal lines**, 3) **lateral lines**, 4) **lateral chevrons**, 5) **transverse bar**. The first three are longitudinal and generally extend posteriorly from T2 or T3. The lateral chevrons extend posterolaterally from the subdorsal area of one segment to near the lateral line on the second segment behind it. These may appear as a series of parallel diagonal lines or chevrons when the larva is viewed from above. In some taxa there is a transverse bar of dark pigment on the first abdominal segment. The transverse bar is always darker than the ground color and is commonly reddish or brown; it varies in extent from a pair of unconnected and relatively small dark dorsal spots, as in *C. (C.) dumetorum, C. (I.) augustus*, and *C. (M.) spinetorum* (figs. 74-4b, -4d, -5c), to a broad band extending across the dorsum toward the lateral line, as in *E. rita* (fig. 74-8d). Variations in this basic pattern of lines result from two factors: 1) each line may be highlighted dorsally and/or ventrally by lines of contrastingly darker or lighter pigment and 2) the degree to which each line and its bordering pigment are developed may vary independently on each segment. Some or all lines may be absent or reduced to discontinuous spots on some or all segments. Monophagous and oligophagous species are usually mono- or oligomorphic while polyphagous species are often polymorphic. These color pattern components (except the transverse bar on A1) are illustrated in figure 1.

KEY TO LAST INSTAR LYCAENIDAE OF CALIFORNIA

1. The most conspicuous body setae clustered on verrucae; some setae on prothoracic shield extending anteriorly over head; A1 spiracles displaced ventrally to a location slightly anteroventral to the lateral verrucae (figs. 30, 69, 70); head not retractable. (Riodininae) 2.

1′ Body setae not arranged in verrucae; no setae on prothoracic shield extending beyond anterior margin of prothorax; spiracles on first abdominal segment in line with those on other abdominal segments (fig. 1); head retractable... 5.

2(1) Segments A1-A7 each with 2 pairs of dorsal verrucae consisting of numerous fine, flexible plumose setae many of which are longer than twice the head width (fig. 70); subdorsal verrucae absent; dorsal and lateral body regions densely covered with echinoid setae (fig. 31)... 3.

2′ Segments A1-A7 each with 1 pair of dorsal verrucae consisting mostly or entirely of short spine-like setae (fig. 30); subdorsal verrucae present on segments T2-A7 (fig. 69); echinoid setae absent... 4.

3(2) Some plumose setae on verrucae apically spatulate (figs. 32, 70); hosts *Baccharis glutinosa* and *Encelia californica*... *Calephelis nemesis*.

3′ Verrucae lacking apically spatulate setae; host *Bebbia juncea*... *Calephelis wrighti*.

4(2′) Dorsal verrucae with darkly pigmented setae; dorsal verrucae on segments A1-A7 (in most populations) also with one nonpigmented plumose setae ca 3X as long as other verrucal setae (fig. 69); hosts *Eriogonum, Krameria,* and *Oxytheca*... *Apodemia mormo*

4′ All setae on dorsal verrucae on segments A1-A7 nonpigmented, spinelike; host *Prosopis*... *Apodemia palmerii*.

5(1′) Eversible tubercles present on A8 (fig. 1) and/or chalazae stellate (figs. 2e, 2f, 2j, 2k, 16, 71) and/or head uniformly black or brown (may be darker around ocelli), ca 1/4 as wide as body; prothoracic shield not pigmented (apparently nonsclerotized)... (Polyommatinae) 45.

5′ Eversible tubercles absent; chalazae not stellate; head often yellowish or bicolored, ca 1/3 as wide as body; prothoracic shield sclerotized, often pigmented and acutely produced anteromedially... 6.

6(5′) Honey gland absent; mushroom setae present on dorsal and lateral body regions (figs. 21-24); prothoracic shield lacking setae lateral to sensory setae (figs. 21, 33-44); chalazae nonsculptured (figs. 2i, 2p)... (Lycaeninae) 7.

6′ Honey gland present on A7 and/or chalazae buttressed (figs. 2n, 2o, 4); mushroom setae absent; prothoracic shield with some setae lateral to sensory setae (figs. 45-54, 61, 64, 67) (Theclinae) 18.

7(3) Prominent setae absent on T2-A9; nearly all setae ca as long as spiracle width, recumbent, truncate; sensory setae often apically truncate-spatulate, at least 3X as long as dorsal setae on T2-A9 (fig.

21); host *Rhamnus crocea* in San Diego Co. and northern Baja California... *Lycaena hermes.*

7′ At least some dorsal setae much longer than spiracle width and/or erect; sensory setae not apically truncate-spatulate, seldom longer than all dorsal setae on T2-A9; host not *Rhamnus crocea*; more widely distributed... 8.

8(7′) Nonprominent dorsal and lateral setae on T2-A6 nonpigmented, mostly ca 2X as long as spiracle width, recumbent, finely tapered (fig. 2i), often appearing whitish; host *Eriogonum*... 9.

8′ Nonprominent dorsal and lateral setae on T2-A6 more erect and/or brownish, shorter, and not finely tapered; host not *Eriogonum*... 10.

9(8) Distinct dorsal prominent setae present on T2-A8; some setae near spiracles on A8 erect, straight and weakly dendritic (fig. 2p)... *Lycaena heteronea.*

9′ Dorsal prominent setae absent or indistinct on T2-A8; setae near spiracles on A8 rarely erect and straight, never dendritic... *Lycaena gorgon.*

10(8′) Dendritic and short clavate-capitate setae present subdorsally and near spiracles on A7, A8 (fig. 15) 11.

10′ No dendritic or clavate-capitate setae subdorsally or near spiracles on A7, A8; on various hosts... 13.

11(10) Head light brown but may be darker anteriorly (fig. 44); legs light brown to nonpigmented; widely distributed mostly below 2000m ... *Lycaena xanthoides.*

11′ Head dark brown, evenly pigmented throughout (figs. 42, 43); legs dark brown; usually found above 2000m in central and northern California... 12.

12(11′) Dorsal and lateral prominent setae on T2-A8 ca 4X as long a spiracles; no more than 25 secondary setae on prothoracic shield, most of which are mushroom setae and the remainder are apically rounded (fig. 42) ... *Lycaena editha.*

12′ Dorsal and lateral prominent setae on segments T2-A8 ca 3X as long as spiracles; at least 30 secondary setae on prothoracic shield of which less than half are mushroom setae and the remainder are mostly tapered (fig. 43)... *Lycaena rubidus.*

13(10′) Head and legs predominantly dark brown (figs. 33, 34); all body setae erect or nearly so, never strongly bent parallel to body surface; alpine species usually found above 3000m; hosts *Oxyria* and *Rumex*... 14.

13′ Legs yellowish or nonpigmented; head yellowish at least near vertex (may be dark anteroventrally); some body setae may be strongly bent nearly parallel to body surface; seldom found above 3000m; on various hosts... 15.

14(13) Dorsal and lateral setae on T2-A8 shorter than sensory setae on prothoracic shield, ca as long as spiracle width... *Lycaena cupreus.*

14′ At least some dorsal and lateral setae on T2-A8 longer than sensory setae on prothoracic shield, ca 2X as long as spiracle width... *Lycaena phlaeas.*

15(13′) Longest dorsal prominent setae on T1 posterolateral to prothoracic shield at most subequal to length of sensory setae; nonprominent setae in same area bent caudad (fig. 23); all or most nonmushroom setae tapered, apically pointed, erect to suberect (fig. 23), rarely bent parallel to body surface; host *Ribes*... *Lycaena arota.*

15′ Longest dorsal prominent setae on T1 posterior to prothoracic shield longer than sensory setae; nonprominent setae in same area bent cephalad (fig. 24); nonprominent lateral setae on T1-A9 often truncate and recurved or bent parallel to body surface; host not *Ribes*... 16.

16(15′) Most nonprominent setae near posterolateral margins of prothoracic shield bent nearly parallel to body surface (figs. 2c, 24); cephalic infuscation extending across frons and posteriorly well beyond ocelli (fig. 36); host *Polygonum douglassii* and perhaps other *Polygonum* and *Rumex* species... *Lycaena nivalis.*

16′ Most nonprominent setae near posterolateral margins of prothoracic shield more erect, seldom bent at less than 45 degrees to body surface; cephalic infuscation less extensive (may be confined to ocelli 1-5); hosts *Polygonum, Rumex*, and Vaccinium... 17.

17(16′) Most nonprominent dorsal setae on T2-A8 tapered, acutely pointed, often bent nearly parallel to body surface; cephalic infuscation limited to an arc enclosing ocelli 1-5 (fig. 40); widely distributed; hosts *Polygonum* and *Rumex*... *Lycaena helloides.*

17′ Most nonprominent dorsal setae on T2-A8 weakly tapered, truncate, less bent (ca 45 degrees to body plane) (fig. 2d); cephalic infuscation often more extensive (fig. 41); found in mountains of central and northern California; host *Vaccinium*... *Lycaena mariposa.*

18(6′) Honey gland absent; dorsal prominent setae present on A7; prolegs with a lateroseries of crochets (fig. 72a); prothoracic shield smoothly convex anteriorly and broadly rounded posterior to sensory setae (fig. 46); hosts *Chrysolepis chrysophylla, Lithocarpus densiflora*, and *Quercus chrysolepis*... *Habrodais grunus.*

18′ Honey gland present; dorsal prominent setae absent on A7; prolegs lacking a lateroseries of crochets; prothoracic shield more-or-less ‘t’-shaped, often acutely produced anteromedially and abruptly narrowed posterior to sensory setae (figs. 45, 47-54, 61, 64, 67)... 19.

19(18′) All dorsal setae erect, straight, and tapered (figs. 7, 8) or recumbent and ca as long as their chalazal width (fig. 2n); sensory setae often with conspicuous lateral spicules (fig. 9)... 20.

19′ Some dorsal setae (at least on A8) clavate-capitate (fig. 2g), strongly bent, or recumbent (inclined caudad) and longer than their chalazal width; sensory setae lacking conspicuous lateral spicules (as in fig. 10)... 38.

20(19) Mushroom lenticles (figs. 8, 26) widely distributed on dorsal and lateral body regions; dorsal prominent setae absent; prothoracic shield white, outlined with black (fig. 45); sensory setae 2-many branched (fig. 6); host *Phoradendron*... *Atlides halesus.*

20′ Mushroom lenticles absent; dorsal prominent setae present or absent; prothoracic shield not white, outlined with black; sensory setae not branched; host not *Phoradendron*... 21.

21(20′) Sensory setae longer than all dorsal setae on T3 (fig. 73), often broadest in apical fourth (fig. 12); nonprominent dorsal setae shorter than or subequal to spiracle width; host *Arceuthobium*... 22.

21′ Sensory setae not longer than all dorsal setae on T3, not distinctly broadest in apical fourth; some dorsal setae on T3 at least 2X as long as spiracle width; not on *Arceuthobium*... 23.

22(21) Sensory setae ca 10X as long as other setae on prothoracic shield and posterolateral to it on T1 (fig. 73); all or most dorsal setae on T2-A6 reclinate, ca half as long as spiracle width, subequal to chalazal width... *Callophrys (M.) spinetorum.*

22′ Sensory setae ca 5X as long as other setae on prothoracic shield and subequal to longest setae posterolaterally adjacent to it; all dorsal setae on T2-A6 erect, mostly 1/2-1X as long as spiracle width and longer than their chalazal width... *Callophrys (M.) johnsoni.*

23(21) Dorsal prominences posterolateral to prothoracic shield well-developed, with longest setae randomly distributed over them (fig. 8); host Cupressaceae... 24.

23′ Dorsal prominences posterolateral to prothoracic shield poorly developed, with longest setae arranged more-or-less in a transverse line (fig. 7); host not Cupressaceae... 27.

24(23) Hosts, *Juniperus californica* and *J. osteosperma* from west end of San Bernardino Mts. west and north in inner Coast Ranges to central California, through Tehachapi Mts. to Walker Pass, and Mojave Desert and Great Basin mountain ranges; also associated with *J. occidentalis* from San Bernardino Mts. northward... *Callophrys (M.) siva.*

24′ Using other hosts and/or found elsewhere... 25.

25(24′) Restricted to vicinity of Otay Mt. in San Diego Co.; host *Cupressus forbesi*... *Callophrys (M.) thornei.*

25′ More widely distributed; host not *C. forbesi*... 26.

26(25′) Host *J. californica* from Mexican border north to San Bernardino and Little San Bernardino Mts.... *Callophrys (M.) loki.*

26′ Hosts *Cupressus sargentii* and *Libocedrus decurrens* (also *J. californica* rarely in inner coast ranges of central California)... *Callophrys (M.) nelsoni.*

27(23′) Cranial infuscation limited to a narrow crescent connecting ocelli 1-5 and not extending to ocellus 6 (figs. 59, 61-64), or much more extensive across front and encompassing all ocelli (fig. 60)... 28.

27′ Cranial infuscation limited to ocellar area, connecting ocelli 1-5 and extending posteriorly to anterior margin of ocellus 6 but not broadly encompassing all ocelli (figs. 65-67)... 35.

28(27′) Cephalic infuscation limited to a narrow band connecting ocelli I-V; host not *Eriogonum* or *Lotus*... 29.
28′ Cephalic infuscation variable; host *Eriogonum* or *Lotus*... 32.

29(28) Frons slightly darker than remainder of head (fig. 64); host *Sedum*... *Callophrys (I.) mossii.*
29′ Fronto-clypeal area not darker than remainder of head; host not *Sedum*... 30.

30(29′) Head width greater than 1.5mm; longest dorsal setae on T2 ca 1.5X as long as sensory setae; host *Pinus*... *Callophrys (I.) eryphon.*
30′ Head width less than 1.5mm; longest dorsal setae on T2 usually less than 1.3X as long as sensory setae; host not Pinus... 31.

31(30′) Ocellar infuscation forming a broad band connecting ocelli 1-5, extending anteriorly along margin of antennal insertion and posteriorly half the distance from ocellus 5 to ocellus 6 (fig. 63); host *Cowania mexicana* in mts. of central and eastern Mojave Desert... *Callophrys (I.) fotis.*
31′ Ocellar infuscation less extensive, not extending anteriorly along margin of antennal insertion and posteriorly half the distance from ocellus 5 to ocellus 6 (fig. 62); absent from mts. of central and eastern Mojave Desert; host not *C. mexicana*... *Callophrys (I.) augustus.*

32(28′) Usually below 1500m throughout cismontane California and the desert slopes bordering the western Mojave and Colorado deserts... *Callophrys (C.) perplexa.*
32′ Found along central coast, in mountains of Mojave Desert, or above 2000m in Sierra Nevada northward... 33.

33(32′) Host *Eriogonum latifolium* (and occasionally *Lotus scoparius*) along coast from Monterey northward to Point Reyes... *Callophrys (C.) dumetorum.*
33′ Not found along coast of central California; host other *Eriogonum* spp.... 34.

34(33′) Found mostly above 2000m in the Sierra Nevada, Siskiyou, and Warner Mts.... *Callophrys (C.) lemberti.*
34′ Found in Mojave Desert mountains... *Callophrys (C.) comstocki.*

35(27) Body with a saw-toothed dorsal profile due to paired dorsal promiences on T3-A6 each with 1 (2 on T2) prominent seta ca 10X as long as spiracles and 3-10X as long as surrounding setae (fig. 56c); hosts *Acacia* and (primarily) *Prosopis*... *Ministrymon leda.*
35′ Body lacking a saw-toothed dorsal profile; dorsal prominences on T2-A6 indistinct or absent; dorsal prominent setae on segments T2-A6 absent or poorly differentiated, no more than 5X as long as spiracles; on various hosts... 36.

36(35′) Chalazae milky, lighter than ground color (best seen in live larvae); host Malvaceae primarily in desert and mountains from San Bernardino Co. southwards... *Strymon columella.*

36′ Chalazae not milky or noticeably lighter than ground color; many hosts but especially Fabaceae, Malvaceae, and Polygonaceae... 37.

37(36′) Restricted to Catalina Island; hosts *Lotus* and *Eriogonum*... *Strymon avalona.*

37′ Widely distributed on many hosts... *Strymon melinus.*

38(19′) Dendritic setae and clavate-capitate, apically truncate setae (fig. 2g) present dorsally on A7 and A8, and laterally on T1, T3, A1, and A7 (between spiracles and margin of honey gland); host *Prunus virginiana*... *Harkenclenus titus.*

38′ At least some dorsal setae on A7 and A8 recumbent, bent, or inclined caudad (fig. 2o), not clavate-capitate; distribution of dendritic setae variable... 39.

39(38′) Head dark brown (except along adfrontal sutures); dendritic setae on T1 lateral to prothoracic shield; all dorsal setae on T2-A6 erect, straight... 40.

39′ Head at least partly yellowish or light brown; no dendritic setae on T1 lateral to prothoracic shield; dorsal setae on T2-A6 variable... 41.

40(39) Legs dark brown; nondendritic dorsal setae on A7, A8 dark brown, acutely tapered, reclinate (nearly parallel to body surface) (fig. 2n); hosts *Ceanothus, Quercus*, and probably other woody perennials... *Satyrium californica.*

40′ Legs nonpigmented; nondendritic dorsal setae on A7, A8 nonpigmented, suberect, often inclined caudad at ca 45 degrees to the body plane, more-or-less clavate and apically rounded (fig. 2o); host *Lupinus*... *Satyrium fuliginosum.*

41(39′) Prominent setae absent on A1-A6; dorsal setae mostly recumbent, broadest near middle, strongly dentate, (fig. 17); dendritic setae present subdorsally on segments T2, T3 (fig. 17); sensory setae at least 3X as long as other setae on and posterolaterally adjacent to prothoracic shield; host *Purshia*... *Satyrium behrii.*

41′ Segments A1-A6 with some prominent setae and/or some dorsal setae erect, cylindric; dendritic setae absent subdorsally on segments T2, T3; sensory setae no more than 2X as long as other setae on and posterolaterally adjacent to prothoracic shield; host not *Purshia*... 42.

42(41′) Prominent dorsal setae on segments T2-A6 erect, straight, orange-brown, forming a pair of dorsal bands each comprised of at least 18 setae per segment (fig. 56a); sensory setae tapered; 2-4 dendritic setae present near sensory setae on prothoracic shield; host *Cercocarpus*... *Satyrium tetra.*

42′ Prominent dorsal setae on T2-A6 less numerous (or absent), variable in pigmentation; sensory setae clavate to tapered; dendritic setae absent on prothoracic shield; host not *Cercocarpus*... 43.

43(42′) Cephalic infuscation limited to a narrow band enclosing ocelli 1-5 (fig. 50); dorsal prominent setae on segments T2-A6 erect, ca 3-4X as long as spiracles, host *Salix*... *Satyrium sylvinus.*

43′ Cephalic infuscation extending across front and posterolaterally at least to ocellus 6 (figs. 49, 51); dorsal prominent setae on T2-A6 absent or 1-2X as long as spiracles; host not *Salix*... 44.

44(43′) Dorsal prominent setae inconspicuous, erect, ca 2X as long as spiracles and other dorsal setae (fig. 56b); all dorsal setae cylindric, orange-brown; sensory setae less than 2X as long as longest setae posterolaterally adjacent to prothoracic shield; host *Quercus*... *Satyrium auretorum.*

44′ Dorsal prominent setae absent or obscure; dorsal and lateral setae of two types: 1) erect, tapered, cylindric, and pale brownish and 2) recumbent, flattened (as in fig. 17), and nonpigmented; sensory setae ca 2X as long as longest setae posterolateral to prothoracic shield; host *Ceanothus*... *Satyrium saepium.*

45(5) Prominent setae only at anterior margin of prothorax; dorsal and lateral setae on T2-A6 recurved, clavate-capitate, ca as long as spiracles; sensory setae tapered; hosts Chenopodiaceae (especially *Atriplex* and *Chenopodium*) and *Sesuvium verrucosum* (Aizoaceae)... *Brephidium exilis.*

45′ At least a few prominent lateral setae on one or more of segments T2-A6 and/or sensory setae not tapered; dorsal and lateral setae on segments T2-A6 variable in structure; host not Chenopodiaceae (except *Atriplex canescens*) or *S. verrucosum*... 46.

46(45′) Sensory setae spatulate or apically broadened (fig. 13)... 47.

46′ Sensory setae finely tapered (fig. 10)... 53.

47(46) Chalazae strongly stellate, lateral points often much longer than basal width of seta (fig. 2e); on various hosts... 48.

47′ Chalazae less stellate, lateral points (if present) seldom longer than basal width of seta (fig. 2j); hosts *Eriogonum* and *Oxytheca*... 49.

48(47) Dorsal setae on T3-A6 erect to suberect or broadly recurved and finely tapered (fig. 2b), not sharply bent near base; dendritic setae only near honey gland; hosts Fabaceae and *Plumbago*... *Leptotes marina.*

48′ Dorsal setae on T3-A6 recumbent, strongly bent near base (fig. 2f); dendritic setae near A1 spiracles and honey gland, and on prothoracic shield; many hosts but not *Plumbago*... *Celastrina argiolus.*

49(47′) Eversible tubercles absent; chalazae not stellate; host *Eriogonum reniforme* or *Oxytheca*... *Philotiella speciosa.*

49′ Eversible tubercles present; chalazae stellate; host various *Eriogonum* species... 50.

50(49′) Head dark blackish brown; legs much darker than body venter, nearly as dark as the head; dorsal prominences on T2-A6 well-defined, each with at least a pair of prominent setae directed posteromedially (fig.

57c); found in Great Basin mountain ranges, the east slope of the Sierra Nevada, and foothills bordering the Mojave Desert; hosts *Eriogonum davidsonii, E. deflexum, E. microthecum, E. plumatella, E. roseum, E. wrightii*, and perhaps *E. heermannii*... *Euphilotes rita.*

50′ Head medium to dark brown; legs nonpigmented to light brown, not nearly as dark as head; dorsal prominences on T2-A6 moderately to weakly developed, with prominent setae directed more posteriorly (fig. 57b) or absent (fig. 57a); host various *Eriogonum* species... 51.

51(50′) At least two dorsal prominent setae on each of segments T2-A6 (fig. 57b); legs lightly pigmented; host *Eriogonum pusillum* or *E. reniforme* in the Mojave Desert from late winter to early summer... *Euphilotes mojave.*

51′ Less than two dorsal prominent setae on each of segments T2-A6 and often none (fig. 57a); legs nonpigmented; host not *E. pusillum* or *E. reniforme*; widely distributed... 52.

52(51′) Host many species of *Eriogonum* but not *E. davidsonii, E. elongatum, E. latifolium, E. nudum*, or *E. wrightii*... *Euphilotes battoides.*

52′ Host many species of *Eriogonum* but not *E. fasciculatum, E. heermannii, E. microthecum*, or *E. ovalifolium* (in California)... *Euphilotes enoptes.*

53(46′) Honey gland and eversible tubercles absent; montane in northern and central California; host Primulaceae, especially *Dodecatheon*... *Agriades franklinii.*

53′ Honey gland present; eversible tubercles present or at least a circle of setae marks the location where they should be; host not Primulaceae 23.. 54.

54(53′) Prolegs lacking a spatulate lobe; segments T2-A6 often with a pair of dorsal prominent setae ca 10X as long as spiracle width; chalazae apparently buttressed (fig. 10); host *Atriplex canescens*... *Plebulina emigdionis.*

54′ Prolegs with a spatulate lobe; setation variable; chalaze not apparently buttressed; host not *A. canescens*... 55.

55(54′) Dorsal setae on T2-A6 mostly erect, tapered to clavate or capitate, shorter than spiracle width; setae around honey gland capitate (fig. 25); host *Dudleya*... *Philotes sonorensis.*

55′ Dorsal setae on T2-A6 variable but not clavate or capitate; setae around honey gland variable; host not *Dudleya*... 56.

56(55′) Lateral margins of spatulate lobes on prolegs pigmented, apparently sclerotized (fig. 72b)... 57.

56′ Spatulate lobes on prolegs nonpigmented, not apparently sclerotized... 58.

57(56′) Nondendritic dorsal setae on A7, A8 erect and straight, or weakly bent (as in Fig. 2j); usually in *Astragalus* seed pods... *Everes amyntula.*

57′ Nondendritic dorsal setae on A7, A8 mostly moderately to strongly bent

(as in figs. 2c, 2k); host various herbaceous Fabaceae including *Astragalus, Lotus*, and *Vicia*... *Everes comyntas.*

58(56′) Dendritic setae present laterally on A6-A8 and/or most subdorsal setae on T2-A6 erect, clavate-capitate (fig. 2j); legs nonpigmented, not darker than body venter; host herbaceous Fabaceae, especially *Astragalus, Lotus*, and *Lupinus*... 59.

58′ Dendritic setae not present laterally on A6-A8; most subdorsal setae on T2-A6 not erect and clavate-capitate; leg pigmentation variable, may be darker than body venter; hosts *Eriogonum* and various Fabaceae... 60.

59(58) Prothoracic shield lacking prominent setae, the sensory setae at least 2X as long as other setae on the shield; most dorsal setae on A7, A8 (between spiracles) moderately to strongly bent (fig. 2k), not capitate; host *Lupinus*... *Glaucopsyche piasus.*

59′ Prominent setae usually present on prothoracic shield, the sensory setae often shorter than some other setae on the shield; dorsal setae on A7, A8 erect, mostly clavate-capitate (similar to fig. 2h) or bent apically (fig. 2j); not only on *Lupinus*... *Lycaeides idas* and *L. melissa.*

60(58′) Dendritic setae present near spiracles on A2; legs not darker than body venter; host *Astragalus, Lotus*, or *Lupinus*... *Glaucopsyche lygdamus.*

60′ Dendritic setae not present on A2; leg color variable; host *Eriogonum* or various Fabaceae... 61.

61(60′) All dorsal setae on T2-A6 erect, straight; leg color variable; host not *Eriogonum*... 62.

61′ Some dorsal setae on T2-A6 recurved or recumbent; legs not pigmented; host *Eriogonum* or Fabaceae... 64.

62(61) Legs nonpigmented, not darker than body venter; dorsal prominent setae in T2, T3 no more than 3X as long as other dorsal setae; widely distributed; host *Lupinus*... *Icaricia icarioides.*

62′ Legs brown, much darker than body venter; dorsal prominent setae on T2, T3 at least 4X as long as other dorsal setae; above 2000m in central and northern California; host not only *Lupinus*... 63.

63(62′) Dendritic setae present in area between honey gland and spiracles on A7; chalazae on prothoracic shield much paler than legs; chalazae anterior to prothoracic shield with lateral points less than 1/4 as long as basal width of chalaza; host *Trifolium*... *Plebejus saepiolus.*

63′ Dendritic setae on A7 only at lateral margins of honey gland; chalazae on prothoracic shield as dark as legs; chalazae anterior to prothoracic shield with lateral points greater than 1/2 as long as basal width of chalaza; host prostrate *Astragalus* and *Lupinus*... *Icaricia shasta.*

64(61′) Dorsal setae on A8 and A9 and nondendritic setae near abdominal spiracles mostly bent parallel to body, broadest near middle, flattened in body plane, and pointed (as in fig. 21)... 65.

64′ Dorsal setae on A8, A9 erect to strongly bent, cylindric, not broadest near middle, and mostly blunt (fig. 2m); nondendritic setae near abdominal spiracles gradually tapered to a blunt tip (as in fig. 2c)... *Icaricia acmon, I. lupini,* and *I. neurona.*

65(64) Longest dorsal prominent seta on T2 as long or slightly longer than longest seta on prothoracic shield; segments T3-A6 usually with at least 4 dorsal prominent setae (fig. 58b); no dendritic setae near spiracles on A1; hosts Fabaceae... *Hemiargus isola.*

65′ Longest dorsal prominent setae on T2 ca 2/3-3/4 as long as longest setae on prothoracic shield; segments T3-A6 usually with only 2 dorsal prominent setae (fig. 58a); dendritic setae present or absent near spiracles on A1; hosts *Eriogonum* and Fabaceae... *Hemiargus ceraunus.*

DIAGNOSTIC SECTION

The larvae of the California lycaenids share several morphological traits which distinguish them from other families of Lepidoptera. These features have been discussed in some detail in the morphology section above. The presence of lenticles, a spatulate lobe on the prolegs, and an onisciform body shape typically separate the California lycaenids from other Lepidoptera larvae. These characters are not without exceptions: lenticles also occur in hesperiids, a spatulate lobe is present on some prolegs of some geometrid moth larvae while absent in two California lycaenids, and the Riodininae are only weakly onisciform.

Riodininae

Most riodinine larvae possess an unusual arrangement of spiracles. Those on the first abdominal segment are displaced anteroventrally far below the latitude of the other abdominal spiracles; they are located slightly anteroventral to the lateral verrucae (figs. 30, 69, 70) and are often hidden by an intersegmental fold.

Other characters which distinguish these larvae from other lycaenid larvae in California are a transverse prothoracic shield with some setae long enough to overhang the head and the most prominent body setae clustered in verrucae. The distribution of verrucae differs in the two genera represented.

The number of larval instars may be variable in all four California riodinines but the minimum (and usual) number for all populations examined is five. Both Dos Passos (1936) and McAlpine (1938) found 8-9 instars in *Calephelis borealis* and *C. muticum*, respectively. It is not certain whether true diapause occurs in any of the four California riodinines but partially grown larvae of *A. mormo, A. palmerii*, and *C. nemesis* were found on their host plants during winter. Larvae of *C. nemesis* were observed to feed briefly (ca one hour) in early afternoon each day during winter when the temperature exceeded 12.8 degrees C. before returning to habitual resting sites on dead foliage. Comstock (1930) also reported intermittent winter feeding behavior in larvae of *A. palmerii*. Some populations of *A. mormo* probably overwinter as ova.

Apodemia

There are two species of *Apodemia* in California. Their larvae have paired dorsal, subdorsal, and lateral verrucae on segments T2-A8 (fig. 69); the prothorax has paired subdorsal and lateral verrucae and a transverse shield which covers most of the dorsum. The verrucae and prothoracic shield primarily contain stiff straight (prominent) setae; these are dark brown in *A. mormo* but much lighter (often non-pigmented) in *A. palmerii*. Several plumose setae arise from each lateral verruca and the prothoracic shield, but are absent from the

subdorsal verrucae. In most populations of *A. mormo* a single plumose seta arises centrally from some or all dorsal verrucae (fig. 69) but these setae are absent from the dorsal verrucae of *A. palmerii*. Additional setae structurally similar to prominent setae on the verrucae, but somewhat smaller and paler, are scattered over the dorsal and lateral body surfaces of both species. Other distinguishing characters include a pale green or pinkish ground color and yellowish head for *A. palmerii* (fig. 74-1b) vs. a predominantly brown or violet-brown ground color (with yellow dorsal and dorsolateral verrucae) and usually brownish head for *A. mormo* (fig. 74-1a).

The most widely distributed species, *A. mormo*, feeds primarily on perennial species of *Eriogonum*, but ova have been collected (and larvae reared) on *Oxytheca perfoliata* (both Polygonaceae). *Krameria* (Krameriaceae) is a host of *A. mormo* in Texas (Kendall, 1976); it is also acceptable to locally collected *A. mormo*. Various populations of *A. mormo* occur throughout California. *Apodemia palmerii* occurs in the southern deserts and feeds on *Prosopis* (Fabaceae).

Calephelis

There are two species of *Calephelis* in California; *C. nemesis* occurs primarily in riparian situations in southern California, while *C. wrighti* occurs in xeric habitats in southern and eastern California. The larval hosts of the former species are *Baccharis glutinosa* and *Encelia californica* (Emmel and Emmel, 1973), while larvae of the latter feed on *Bebbia juncea*, all in the Asteraceae. The larval ground color of both species is cream or buff (fig. 74-1c). They have one pair of dorsal verrucae on T2, T3, and A8, but two pairs on A1-A7; subdorsal verrucae are absent, but a single pair of lateral verrucae occurs on T1-A8 (fig. 70). The verrucae consist mostly of very long, slender, nonpigmented or pale brown plumose setae which give the larva a feather-like appearance; similar setae occur on the prothoracic shield. There are no straight, stiff, spine-like setae as in *Apodemia* but echinoid setae (fig. 31) cover most of the lateral body areas. The head is yellowish with a small amount of brownish mottling. In *C. nemesis* many plumose setae (ca 1/4-1/2 as long as the longest ones) on each verruca are broadly spatulate apically (figs. 32, 70), while in *C. wrighti* no spatulate setae occur. In both species a few short, clavate, plumose setae are present on the dorsal verrucae and often near the spiracles. These are mostly nonpigmented, but those on the dorsal verrucae on segments A1 and A7 are often black (especially in *C. wrighti*).

Lycaeninae

The Lycaeninae is one of the smallest yet widely distributed lycaenid subfamilies and may be better represented in California (twelve species) than in any other region of equivalent size. Most local species are

univoltine, diapause as ova, and use host plants in the Polygonaceae. For many years these were placed in the genus *Lycaena*, but Miller and Brown (1979) divide them among six genera. On the basis of similar biology and/or morphology of immature stages, it is convenient to discuss them as five groups which do not coincide with the generic arrangement of Miller and Brown (1979). Pending further comparative studies, we retain the single genus *Lycaena* for the group.

Lycaena

The larvae of all members of this genus lack a honey gland and eversible tubercles. The length of the prothoracic shield is about twice as great as its width. It is acutely pointed at the anterior, posterior, and lateral extremities and is generally diamond-or 't'-shaped (figs. 33-44). Although the width is greatest along the line of the sensory setae (in the anterior third), there is typically a second lateral expansion in the posterior third. Prominent setae are absent from the prothoracic shield; other secondary setae on it are much shorter than the sensory setae and never occur lateral to them. The sensory setae usually appear finely tapered and devoid of lateral spicules; but minute lateral spicules (visible with SEM) may occur near the apex in some species such as *L. mariposa*. Mushroom setae, which are unique to this group, are scattered over the dorsal and lateral body regions. Although mushroom setae may occur as early as the second instar, they are more likely to appear first in the third or fourth instar. Dendritic setae are present only in *Lycaena editha, L. heteronea, L. rubidus*, and *L. xanthoides*. The chalazae of all setae are nonsculptured or very weakly buttressed. Typically, a latero-series of crochets (in addition to the mesoseries) occurs on the prolegs but it may be greatly reduced or absent on some prolegs. *Lycaena editha, L. rubidus*, and *L. xanthoides* typically have three mandibular setae (*L. xanthoides* rarely has up to five) while the other *Lycaena* species typically have two mandibular setae. But in some populations of *L. gorgon* and *L. heteronea* there may be three mandibular setae.

Two species which differ similarly in larval morphology and biology from the others are *L. cupreus* and *L. phlaeas*. In California both occur mostly above 3000m, are univoltine, and typically have four larval instars; *L. phlaeas* sometimes has five instars. Both species probably diapause as larvae. When reared from ova in the lab at 25-27 degrees C. some larvae of *L. cupreus* often complete development but most enter diapause in the third instar. Under the same conditions *L. phlaeas* is continously brooded. In nature mature larvae of both species were found in mid-July and younger larvae in August. In California the larvae of *L. cupreus* are associated with *Rumex*, especially *R. paucifolius*, and larvae of *L. phlaeas* are associated with *Oxyria digyna*. Elsewhere *L. cupreus* has also been reported to utilize *O. digyna*, while *L. phlaeas* often uses *Rumex* (Ferris, 1974). The ground color of both species is green in California, but *L. phlaeas* larvae from Asia and Europe may be

pink or green and some California (and Old World) specimens have a pinkish dorsal and/or lateral line (fig. 74-3b). In California they are distinguishable from other *Lycaena* species by their darkly pigmented head and legs, pale prothoracic shield (figs. 33, 34), and lack of prominent dorsal setae. All dorsal and lateral setae on T2-A8, aside from mushroom setae, are uniformly short, erect, tapered, and brownish. In California *L. cupreus* larvae these setae are shorter than the sensory setae and about as long as the spiracle width, while in *L. phlaeas* at least some are longer than the sensory setae and about twice as long as the spiracle width. Larvae of *L. cupreus snowi* (Edwards) from Colorado have setae about as long as those of *L. phlaeas*. Larvae of *L. phlaeas* examined from Corsica, Japan, and the eastern U.S. are similar to California specimens in setation but have much lighter crania and legs.

Another group with similar biologies and larval morphology consists of *L. editha, L. rubidus*, and *L. xanthoides*. Larvae of all three feed on *Rumex* and are myrmecophilous; old records of *L. editha* larvae feeding on *Horkelia* and *Potentilla* (Rosaceae) (reiterated by Johnson and Balogh, 1977 and Pyle, 1981) are not supported by our observations. The ground color of these larvae varies from green to maroon or rust-red and often there is a maroon middorsal line (fig. 74-3c). All dorsal and lateral setae are erect to suberect and, except for mushroom setae, brownish. The most distinctive features of these larvae are well developed dendritic setae near the spiracles, especially on T1, A7, and A8 and short clavate-capitate setae dorsal to the spiracles, especially on A7 and A8 (fig. 15). In each species the cranium and prothoracic shield are dark; *L. editha* and *L. rubidus* also have dark legs. The head and prothoracic shield of *L. xanthoides* are lighter than in the other species (figs. 42-44); dendritic setae usually occur only near the spiracles on T1, A7, and A8, but in some populations these setae also occur on A1-A4. In *L. editha* and *L. rubidus* larvae dendritic setae are present near the spiracles on T1, A7, A8, at least some of segments A1-A6, and frequently laterally on T2 and T3. The larvae of *L. editha* and *L. rubidus* differ in prothoracic shield setation as described in the key. *Lycaena editha* and *L. rubidus* are sometimes sympatric and occur mostly above 2000m in central and northern California but *L. xanthoides* is more widely distributed, mostly below 2000m, and does not occur with the others. Adults of *L. editha* found below 2000m in the vicinity of Mount Shasta are similar (especially in size) to *L. xanthoides* and have been considered intermediate between those species (Scott, 1980); but larvae from this population (at Dunsmuir and Mount Shasta City) are more similar to Sierra Nevadan *L. editha* and key to that species.

Two other closely allied species are *L. gorgon and L. heteronea*. They are distinguished from the other *Lycaena* species by the use of *Eriogonum* as a larval host and by the presence of numerous nonpigmented, recumbent setae at least twice as long as the spiracles. These setae have a finely granular surface giving them a whitish appearance. The larval

color is pale turquoise to green for *L. gorgon* (fig. 74-2a) and dull blue-green to green for *L. heteronea* (fig. 74-2c); both species are faintly mottled but devoid of strongly contrasting markings; some *L. heteronea* larvae have a pale yellow or white lateral line. The cranium is nonpigmented in *L. gorgon* (fig. 37) and nonpigmented to somewhat brownish in *L. heteronea* (fig. 38). *Lycaena heteronea* occurs mostly above 1500m from Mount Pinos in Ventura Country northward through the Sierra Nevada, Cascade, and Warner ranges and at sea level along the coast near Point Reyes. *Lycaena gorgon* is primarily cismontane in distribution below 1500m but also occurs up to about 2000m along the east slope of the Sierra Nevada from southern Mono County southward and in the Warner Mountains.

Usually these species are easily distinguished according to their setation. *Lycaena heteronea* has distinct dorsal prominent setae (usually somewhat melanic) on T2-A8 and erect dendritic setae near the spiracles on A7 and A8 (also occasionally on T1 and rarely on the prothoracic shield); nonprominent dorsal setae are mostly 1.5-2X as long as the spiracle width. *Lycaena gorgon* lacks both prominent dorsal setae and dendritic setae; the dorsal setae are mostly 2-4X as long as the spiracle width. But in *Lycaena gorgon* larvae from the Warner Mountains of Modoc County the setae are more erect (recumbent to suberect) than in larvae from elsewhere and some dorsal setae may be nearly as erect as the dorsal prominent setae of *L. heteronea*. Occasionally, they also have 1-2 erect (but not dendritic) setae near the A7 and A8 spiracles. Larvae of *L. heteronea* from near Mount Lassen resemble those of *L. gorgon* from the Warner Mountains in setal erectness; their dorsal prominent setae are less erect and less distinct than in other populations of *L. heteronea* and are nonpigmented. In these larvae the dendritic setae near the spiracles on A7 and A8 are poorly developed; there may be only 3-4 of them and with lateral spicules very short and confined to the apex. In both of these populations the mandibles frequently have three setae but other populations of both species typically have two mandibular setae.

Lycaena hermes larvae differ greatly from those of the other *Lycaena* species in host, range, and morphology. They feed on *Rhamnus crocea* (Rhamnaceae) and are restricted to San Diego County and northern Baja California, Mexico. They are bright, light green without strongly contrasting markings (fig. 74-2b), though a pair of pale yellowish dorsal lines may be present. These larvae may appear glabrous since all dorsal and lateral setae on T2-A8 are sparsely scattered, subequal in length to the spiracles, and recumbent; the setae are lightly pigmented and weakly tapered to blunt-tipped. The sensory setae on the prothoracic shield are at least twice as long as all other dorsal and lateral setae on T2-A8 and subequal to the longest setae at the anterior margin of the prothorax; they may be filiform or tapered, as in other *Lycaena* species, or apically truncate-spatulate (fig. 21). The cranium is nonpigmented and the prothoracic shield is rather small and narrow (fig. 39).

The larvae of the four remaining *Lycaena* species are similar in setation but different in biology. *Lycaena helloides* and *L. nivalis* feed on *Polygonum* and (at least in the lab) *Rumex* (Polygonaceae); some populations of *L. helloides* also feed on *Potentilla* (Rosaceae) (Shapiro, 1974). *Lycaena arota* feeds on *Ribes* (Saxifragaceae) and *L. mariposa* feeds on *Vaccinium* (Ericaceae) (Pratt and Ballmer, 1986). They have well-defined dorsal prominent setae on T2-A8 while most other dorsal and lateral setae (not mushroom setae) on T2-A8 are erect to recumbent and more-or-less tapered but apically truncate (figs. 2c, 2d). In *L. arota* dorsal setae on T2 posterolateral to the shield are curved caudad (fig. 23) while in the other species these setae are curved cephalad (fig. 24). The ground color is green for all four species. Some populations of *L. arota* (especially in southern California) have white or yellowish paired dorsal and lateral lines (fig. 74-1d). Larvae of *L. nivalis* sometimes have a maroon middorsal line and an indistinct yellowish lateral line (fig. 74-3a); some larvae of *L. helloides* and *L. mariposa* also have an indistinct yellowish lateral line (fig. 74-2d). Cephalic infuscation in *L. nivalis* extends across the front of the head and posteriorly well beyond the ocelli (fig. 36), while in *L. arota* (fig. 35) and *L. helloides* (fig. 40) it is limited to a narrow cresent connecting ocelli 1-5. In *L. mariposa* (fig. 41) cephalic infuscation varies from nearly as extensive as in *L. nivalis* to virtually absent. Although *L. helloides* is multivoltine (diapause stage not known) and widely distributed (mostly below 2000m) the others are univoltine and mostly confined to higher elevations in central and northern California.

Theclinae

The most distinctive features of the California thecline larvae are the head width (ca half as great as the body), lack of eversible tubercles, and presence of buttressed chalazae. The prothoracic shield is sclerotized, frequently brownish, and lacks secondary setae longer than the sensory setae; the head color ranges from yellowish to dark brown. The single representative of the tribe Theclini, *H. grunus*, lacks a honey gland, has a broadly diamond-shaped prothoracic shield (broadly rounded posterior to the sensory setae), five mandibular setae, and a biordinal lateroseries of crochets. All other species belong to the tribe Eumaeini. They have a honey gland, a more-or-less 't'-shaped prothoracic shield (abruptly constricted posterior to the sensory setae), usually two mandibular setae, and lack crochet lateroseries on the prolegs. In general appearance, thecline larvae (especially *H. grunus*) are most similar to those of the Lycaeninae; they may be distinguished from the latter by the presence of buttressed chalazae, setae on the prothoracic shield lateral to the sensory setae, usual presence of a honey gland, and absence of mushroom setae.

Among the Eumaeini two groups may be distinguished according to setation. In one group consisting of *Atlides, Callophrys, Ministrymon*, and *Strymon* all setae are cylindric, tapered, and straight or slightly

curved with dendritic setae absent or inconspicuous (often poorly developed or obscure) and confined to the margins of the honey gland. Also in this group, the sensory setae are filiform to slightly clavate (branched in *Atlides*) and often have conspicuous lateral spicules; the mandibles have two setae. The other group, consisting of *Harkenclenus* and *Satyrium*, has a broad range of setal forms including erect, recurved, tapered, and clavate; dendritic setae occur prominently around the honey gland and often on other segments, while other dorsal setae on A7 and A8 are often recumbent or somewhat capitate. Also in this group, the sensory setae are filiform, tapered, or spatulate and have inconspicuous lateral spicules; the mandibles have 2-6 setae. Coincidentally, diapause occurs as pupae in the former group and as ova in the latter. Most California thecline species are univoltine and restricted to a few closely related larval hosts. A few species are bi- or trivoltine, while only *S. melinus* is continuously brooded and known to utilize a wide range of larval hosts.

Atlides

The single California species, *A. halesus*, occurs throughout the state but is more abundant in the south. It is often encountered in lowland riparian habitats where the larval mistletoe host may be abundant. Features which distinguish larvae of this species from other California theclines include a velvety texture due to an even distribution of short reddish-brown setae (no prominent setae), uniform green color (fig. 74-4a) (rarely obscurely mottled), presence of mushroom chalazae (fig. 26), branched sensory setae (fig. 6), a white prothoracic shield outlined in black (fig. 45), and use of *Phoradendron* (Viscaceae) as a larval host. There are 3-4 annual broods in the south, but probably 2-3 in the north; the pupae overwinter.

Callophrys

The genus *Callophrys* was redefined by Clench (1961) to contain six subgenera three of which (*Callophrys, Incisalia*, and *Mitoura*) occur in california; some authors including Miller and Brown (1981) give these taxa full generic status. The systematics of this group is in need of review and it seems unlikely that any study lacking comprehensive biological, morphological, and/or biochemical data can resolve existing controversies. The morphology of mature larvae is useful in distinguishing some subgenera, but of little use in distinguishing most species. Yet the taxonomic limits of both species and subgenera are often definable by biological differences such as host preference, habitat selection, and number of instars.

In California, we provisionally recognize four species each in the subgenera *Callophrys* and *Incisalia* and six in *Mitoura*; Scott (1986) recognizes only three species each of *Callophrys* and *Mitoura* in

California, but his evidence is not compelling. Adding to the confusion is a recent nomenclatural change; the name *C. dumetorum*, previously applied to most lowland *Callophrys* populations in California, properly refers only to those along the central coast previously known as *C. viridis* (W. H. Edwards), which is now relegated to a junior synonym (J. F. Emmel, *in litt.*). The name *Callophrys perplexa*, formerly considered the southern California subspecies of *C. dumetorum* (in its former usage), now becomes the senior synonym and must be applied to the remaining lowland cismontane populations of this species.

There is little difference in larval morphology among the California species of *Callophrys* and *Incisalia* (and also *Strymon*). All are covered with erect, straight, tapered setae of varying lengths which are non-pigmented or pale brown and apically darkened. Prominent setae on T2-A6 are absent or obscure. The sensory setae are filiform to slightly broader in the apical half and have conspicuous lateral spicules (fig. 7); rarely one or both may be bifurcate. Dorsal prominences on T2-A6 are weakly to moderately developed, while those on T1 anterior and posterior to the prothoracic shield are weakly developed. The most prominent dorsal setae on T1 posterolateral to the shield are arranged in one or two transverse rows (fig. 7). Relatively inconspicuous dendritic setae occur near the honey gland. The head is yellowish-brown with darker pigment confined to an arc connecting ocelli 1-5 but not extending to ocellus 6 (fig. 59) or the entire anteroventral half of the head may be dark brown, broadly enclosing all ocelli (fig. 60).

Mitoura larvae are easily distinguishable from those of the other subgenera. Those species which utilize Cupressaceae as a larval host have well developed dorsal prominences on T1 anterior and (especially) posterior to the prothoracic shield often causing it to appear sunken; the most prominent setae on the prominences posterior to the shield are randomly distributed (fig. 8); dendritic setae are absent. In those species which utilize Viscaceae as a larval host the dorsal prominences on T1 posterior to the shield are poorly developed and have prominent setae arranged in a transverse row (as in the other subgenera) or absent (fig. 73); but distinct dorsal prominences are present at least on T2 and A6; they also have dendritic setae near the honey gland.

No consistent morphological distinctions were found to separate larvae of *Callophrys* and *Incisalia*. Larvae of species in these subgenera are best distinguished according to distribution and host plant. In California *Callophrys* larvae utilize *Eriogonum* (Polygonaceae) and *Lotus* (Fabaceae), while *Incisalia* larvae feed on various hosts in other plant families. There are four larval instars in all species of these subgenera in California.

Cephalic pigmentation is useful in distinguishing some *Callophrys* populations. Larvae of *C. dumetorum* (formerly *C. viridis*) from near San Francisco and *C. perplexa* (formerly *C. dumetorum*) from southern California have dark cephalic pigment narrowly confined to ocelli 1-5

(fig. 59). In larvae of most other California *Callophrys* populations the head is dorsally yellowish-brown and ventrally dark brown with dark pigment broadly enclosing all ocelli (fig. 60), but larvae of *C. dumetorum* from near Monterey are variable in cephalic pigmentation. The dorsal profile can also be used to discriminate some taxa. The dorsal prominences in *C. comstocki, C. dumetorum*, and *C. lemberti* often (but not invariably) create a saw-toothed profile (fig. 74-4b), while those in *C. perplexa* are more rounded (fig. 74-4c). All the *Callophrys* species use *Eriogonum* as a larval host; *C. perplexa* also commonly uses *Lotus crassifolius* and *L. scoparius; C. dumetorum* is reported to use *L. scoparius* in the San Francisco area (Gorelick, 1971). *Callophrys comstocki* occurs in several Mojave Desert mountain ranges; *C. perplexa* occurs throughout cismontane California up to ca 1500m; *C. lemberti* occurs generally above 2000m in the Cascade, Sierra Nevada, Siskiyou, and Warner Mountains; *C. dumetorum* is strictly coastal and associated with *Eriogonum latifolium* from northern Monterey County to Sonoma County (G. Gorelick, personal communication). Although *C. comstocki* is at least partially bivoltine, the other species are univoltine. Larval ground color is usually green, pale pink, or yellow; dorsal and lateral lines and dorsolateral chevrons may be present or absent.

Morphological differences among *Incisalia* larvae are too small to aid greatly in identification. The larval morphology of *I. eryphon* is most divergent, as indicated in the species key. But the larvae of all the species are best identified according to host and locality. As with some members of *Callophrys*, the *Incisalia* larval head is yellowish-brown with dark pigment confined to a narrow arc linking ocelli 1-5. Larvae of *I. augustus*, the most widespread species, can be found in most areas except the deserts on several hosts, especially *Adenostoma, Heteromeles, Prunus* (all Rosaceae), *Ceanothus, Rhamnus* (both Rhamnaceae), and *Cuscuta* (Convolvulaceae); Powell (1968) also confirms that it uses *Arbutus menziesii* Pursh. (Ericaceae) and *Chlorogalum pomeridianum* (D. C.) Kunth. (Liliaceae). Larvae of *I. eryphon* occur on *Pinus* (Pinaceae) usually above 2000m from the San Bernardino Mountains northward through the Cascade, Sierra Nevada and Siskiyou Mountains. Larvae of *I. fotis* feed on *Cowania mexicana* var. *stansburiana* (Rosaceae) in mountains of the Mojave Desert. Larvae of *I. mossii* feed only on Crassulaceae; primarily they utilize *Sedum* but some populations also use *Dudleya* (J. F. Emmel, personal communication); this species occurs in isolated cismontane colonies from the San Bernardino Mountains northward. *Incisalia augustus* is partially bivoltine, especially in the south, but the other species of *Incisalia* are univoltine.

Coloration can be useful in identifying live larvae of some *Incisalia* species. Larvae of *I. augustus* (fig. 74-4d) and *I. fotis* are polymorphic and often resemble members of the nominate subgenus. Their ground color is usually green and they frequently have white or red and white dorsolateral chevrons and lateral lines; and they often have at least a

trace of a reddish lateral bar on A1 (fig. 74-4d). Larvae of *I. mossii* are red or greenish-yellow and may have whitish lateral chevrons. Larvae of *I. eryphon* are monomorphic with a green ground color and paired yellowish white dorsal and lateral lines (fig. 74-5a).

The *Mitoura* species can be divided into two groups based on biology and larval morphology (as described above). Those which feed on cedar, cypress, and juniper (Cupressaceae) have 5–7 larval instars, whereas those which feed on dwarf pine mistletoe (Viscaceae) have five larval instars. The Cupressaceae-feeders have well developed dorsal prominences on T1 anterior and (especially) posterior to the prothoracic shield but segments T2-A6 are dorsally rounded, lacking prominences. These larvae are dark green with white dorsal and lateral lines which are weakened or broken intersegmentally, as illustrated for *C. (M.) nelsoni* (fig. 74-5b); they are densely covered with erect straight setae ca twice as long as the spiracle diameter; dendritic setae are absent. The Viscaceae-feeders are more angulate with paired dorsal prominences at least on T2 and A6 and weak lateral prominences along the lateral fold (best developed on A7 and A8); but dorsal prominences on T1 are poorly developed or absent (fig. 73). All dorsal setae (except those surmounding dorsal prominences) are shorter than the sensory setae and at most subequal in length to the spiracle width. Prominent setae subequal in length to the sensory setae are present on T1 posterolateral to the prothoracic shield in *C. (M.) johnsoni* but not in *C. (M.) spinetorum*. The ground color of these larvae is yellow to olive-brown, while the dorsal prominences are usually brighter yellow, bordered laterally by white and dark brown, and often reddish apically (fig. 74-5c). A transverse bar may be apparent as a darkening of the dorsal prominences on A1. These larvae appear to glisten due to a shinier body surface and shorter, sparser setae than in the Cupressaceae-feeders; their setae are often reclinate toward the apices of the dorsal prominences (fig. 4); a few inconspicuous dendritic setae occur at the margin of the honey gland.

The California *Mitoura* species which feed on Cupressaceae comprise a portion of a complex of several often narrowly allopatric sibling species and/or subspecies occurring throughout most of North America. These may be poorly distinguishable where their ranges converge and are perhaps best considered ecotypic components of a superspecies. Yet in spite of a few areas of possible intergradation (Shields, 1985; Scott, 1986), the California taxa are relatively uniform throughout their ranges which may be parallel and narrowly separate (by altitude and habitat) over long distances. Thus, *M. nelsoni* occurs in association with *Libocedrus decurrens* in montane habitats from San Diego County to Oregon, while *M. loki* and *M. siva* often occur at different elevations and in association with other hosts in the same mountains. The larvae of these species are best distinguished according to host and locality.

Although larvae of most (probably all) of the Cupressaceae feeders can be reared on many plants in that family, most populations are

associated with one host species in nature (Johnson, 1978). Four subspecies of *M. siva* occur in California; *M. s. siva* is associated with *Juniperus osteosperma* in the mountains of the eastern Mojave Desert; *C. (M.) s. juniperaria* (J. A. Comstock) is associated with *J. californica* from the lower northwest slopes of the San Bernardino Mountains westward along the northern edge of the San Gabriel Mountains (where it is also associated with *J. osteosperma*) to the eastern edge of the Tehachapi Mountains; *C. (M.) s. mansfieldi* (Tilden) is associated with *J. californica* in the inner coast ranges from Ventura County to San Benito County; *C. (M.) s. chalcosiva* Clench is associated with *J. occidentalis* in the Inyo and White Mountains. The status of brown *M. siva* (or *M. nelsoni*) populations associated with *J. occidentalis* in the San Bernardino Mountains, Sierra Nevada, and Modoc County is uncertain; these may be conspecific with *C. (M.) barryi* Johnson described from eastern Oregon. There are two subspecies of *Mitoura nelsoni*; the nominate one ranges from the mountains of San Diego County northward in association with *Libocedrus decurrens; C. (M.) n. muiri* (Hy. Edwards) is associated with *Cupressus sargentii* and (rarely) *J. californica* (J. Lane, personal communication) in coastal mountains from San Luis Obispo County to Mendocino County. *Mitoura loki* occurs with *J. californica* from the eastern San Bernardino Mountains southward to Baja Californica. *Mitoura thornei* is known only from Otay Mountain in San Diego County in association with *Cupressus forbesii. Mitoura nelsoni* is univoltine, but at least some populations of the other species are partially bi- or trivoltine.

Habrodais

One species of *Habrodais, H. grunus*, occurs in montane habitats throughout California except in the deserts. The larval hosts are *Quercus chrysolepis* and, according to Pyle (1981), *Q. vaccinifolia* Kell., *Chrysolepis chrysophylla* (Dougl.) A. DC., and *Lithocarpus densiflora* (H. & A.) Rehd., all in the Fagaceae. *Habrodais grunus* is the only California member of the tribe Theclini and differs considerably from the other theclines. The most obvious differences are the lack of a honey gland, presence of a lateroseries of crochets (fig. 72a), and an evenly convex posterior margin of the prothoracic shield (fig. 46). It also lacks dendritic setae and the sensory setae are finely tapered with minute lateral spicules confined to the apex. The ground color is pale blue-green (including the prothoracic shield) and a pair of pale yellow subdorsal lines may be present (fig. 74-3d). A pair of prominent dorsal setae occurs on segments T2-A8, while other dorsal setae are bent parallel to and flattened in the body plane. This species is univoltine with egg diapause.

Harkenclenus

The single member of this genus, *H. titus*, ranges from coast to coast but in California it is confined to the northeastern corner southward in the

eastern Sierra Nevada to near Lake Tahoe. Larvae feed on *Prunus virginiana* and are distinctively marked reddish dorsally on T2, T3, and A6 and dorsally and laterally on A7-A10; the remainder of the body is green (fig. 74-5d). The head is dark brown in a band across the frons and posteriorly to the ocelli, but lighter dorsally (fig. 47). Aside from some members of *Satyrium*, this is the only California thecline with dendritic setae present beyond the margin of the honey gland on A7. Dendritic setae occur laterally near the spiracles or in that latitude on T1-A1, A7, and A8, with the greatest numbers (ca 20) on T3 and A1. All setae are orange-brown, erect, and straight. Prominent setae on T2-A6 are indistinct, but the longest setae (dorsally and along the lateral fold) are ca 2.5X as long as the spiracle diameter. This species is univoltine with egg diapause.

Ministrymon

One member of this genus, *M. leda*, inhabits the southern California deserts. It is multivoltine and larvae feed primarily on *Prosopis* but we have one record on *Acacia greggii* (both Fabaceae). They are distinctively marked green and white (fig. 74-6a) and segments T2-A6 have dorsal prominences which confer a saw-toothed dorsal profile (fig. 56c). Each dorsal prominence is surmounted by 1-4 prominent setae ca 3-4X as long as the spiracle diameter; most other dorsal setae are 1-2X as long as the spiracle diameter.

Satyrium

Seven members of this genus occur in California; all are univoltine with egg diapause. Although morphologically more diverse than other California thecline genera, the *Satyrium* species are united by the presence of at least 20 dendritic setae on A7, especially along the margin of the honey gland; four species also have dendritic setae on other segments. Among other California theclines only *H. titus* shares such an abundance of dendritic setae. Distinct dorsal prominences may be present, but more often there are weakly developed dorsal ridges extending from T2-A6, so that in cross-section the body appears trapezoidal with the dorsal area flat or somewhat concave and the lateral areas sloping outward to the lateral folds. Prominent setae of variable number and degree of distinctness occur along the dorsal ridges and the lateral fold. Other setae may be recumbent to erect and nonpigmented to dark brown. Cephalic pigmentation varies from yellow to dark brown.

Satyrium auretorum occurs throughout cismontane California in chaparral and scrub oak woodland. Larvae feed on various oaks, especially the scrub oaks, *Quercus cornelius-mulleri, Q. dumosa*, and *Q. wislizenii*. They are green with a yellow lateral line of variable intensity and often ventrally bordered with pink (best developed on T2, T3, A7 and A8) (fig. 74-6b). The head is dark brown anteroventrally (across the frons and extending posterolaterally beyond the ocelli), but yellowish

brown apically (fig. 51). The sensory setae are tapered, ca 5X as long as other setae on the shield, and 1.5X as long as the longest dorsal setae posterolaterally adjacent to the shield. Prominent dorsal and lateral setae, ca 2X as long as the spiracle width, occur in groups of 2-10 on T2-A6 (fig. 56b). Nonprominent dorsal and lateral setae on T2-A6 are weakly spindle-shaped, suberect, straight to moderately bent, and ca 1-1.5X as long as the spiracles; on A7 they are shorter and more strongly bent (often parallel to the body). These setae are reddish brown, minutely dentate, and tapered. Dendritic setae are confined to A7.

Satyrium behrii ranges from the Little San Bernardino Mountains west to the Mount Pinos area, northward along the east slope of the Sierra Nevada to Oregon, and in the Panamint and White Mountains. The larvae feed on *Purshia glandulosa* and *P. tridentata*. The ground color is dark green with white or yellow middorsal and lateral lines and dorsolateral chevrons on T2-A6 (fig. 74-6c). The head is mostly yellowish brown, but dark pigment extends across the frons and posterolaterally beyond the ocelli (fig. 52). A pair of prominent dorsal setae ca 3-4X as long as the spiracle width occurs on T2; lateral prominent setae are present on A7 and A8 but usually absent elsewhere. Most other dorsal and lateral setae are 1-2X as long as the spiracle width, bent parallel to and flattened in the plane of the body surface, and acutely tapered. Dendritic setae occur in groups of 4-6 subdorsally on T2 and T3 as well as around the honey gland.

Satyrium californica occurs throughout the state except in the eastern deserts. Larvae have been found on *Ceanothus* and *Quercus*, but additional hosts are likely since the butterfly sometimes occurs in the absence of those plant genera. The ground color is chocolate brown dorsally and white ventrally (fig. 74-6d); the head (fig. 53), legs, chalazae, and most setae are dark brown. Conspicuous dendritic setae ca 1-3X as long as the spiracle width are present on T1-A7. While dorsal and lateral prominent setae on T2-A6 are ca 5-7X as long as the spiracle width, other dorsal and lateral setae on those segments are sparse and 1/4-1X as long as the spiracle width. Since larvae are usually found in early morning they may be nocturnal, as with *S. edwardsii* (Grote and Robinson) in the eastern United States (Webster & Nielson, 1984).

The larva of *S. fuliginosum* superficially resembles that of the polyommatine *I. icarioides* in habits and appearance more than the larvae of its congeners. The ground color is light green with whitish lateral chevrons (fig. 74-7a), the head is dark brown (fig. 48), and the body dorsum is evenly convex. Dorsal prominent setae (ca 2-5X as long as the spiracles) are present on T2 but absent or obscure posteriorly; lateral prominent setae are more abundant and conspicuous on T1-T3 and A6-A10 but may be absent on the intervening segments. Dendritic setae ca 2X as long as the spiracles are present posterolateral to the prothoracic shield, near the spiracles (or in the same latitude) on T3-A6, and around the honey gland. The remaining dorsal and lateral setae are

numerous, ca .5-IX as long as the spiracles, erect, tapered, and light brown. The larvae feed on *Lupinus* and are strongly myrmecophilous; they probably feed nocturnally, but during the day they can be found at the base of host plants and under nearby rocks. This species occurs along the eastern slopes of the Sierra Nevada northward through the Cascade, Siskiyou, and Warner Mountains.

The larva of *S. saepium* differs from its congeners (except *S. auretorum* and *S. sylvinus*) in having dendritic setae confined to the lateral margins of the honey gland. These setae are ca as long as the spiracles, clavate, and have very short lateral spicules. The following combination of characters distinguish this species from all others: the sensory setae are slightly spatulate in the apical fourth, ca 4-5X as long as the spiracles and nearly all other dorsal and dorsolateral setae on T2-A6; prominent dorsal setae are absent; the dorsal and lateral setae are of two forms intermixed, one of which is brownish, suberect, and cylindric and the other is nonpigmented, coarsely dentate, spindle-shaped, basally bent nearly parallel to the body surface, and compressed in that plane (as in fig. 18). Dendritic setae occur only on A7. The ground color is dull, dark green; a yellow lateral line extends from T2 to A10 and is most prominent on A8. Cephalic infuscation is limited to a diffuse band across the ocellar region (fig. 49). Larvae feed on *Ceanothus* and occur throughout the state except in the eastern deserts.

Satyrium sylvinus is also widespread in California, but absent from the Colorado and Mojave Deserts. Larvae feed on *Salix* (Salicaceae). They are light green with distinct white subdorsal and lateral lines and somewhat less distinct lateral chevrons (fig. 74-7b). The head is yellowish with dark pigment confined to a narrow band connecting ocelli 1-5 (fig. 50). The sensory setae are finely tapered, ca 3-5X as long as the spiracles and other setae on th shield, and subequal to the longest dorsal prominent setae posterolateral to the shield and on T2. Dorsal prominent setae on T3-A6 are ca 2X as long as the spiracles and other dorsal and lateral setae on those segments. All setae are tapered, suberect, and nonpigmented. Nonprominent dorsal and lateral setae on T2-A6 are erect to strongly bent; those on A7 are often bent parallel to the body. Dendritic setae are confined to A7. The body is somewhat angulate in cross-section due to a rather flat or slightly concave dorsum (less noticeable in distended specimens).

Satyrium tetra has about the same distribution as *S. saepium*, being found in chaparral habitats containing its host, *Cercocarpus* (Rosaceae). Larvae resemble those of *S. sylvinus* in coloration, but have less well developed dorsal and lateral lines and more prominent lateral chevrons (fig. 74-7c). A slightly broader band of dark pigment surrounds the ocelli (fig. 54). They are also distinctive in being covered with erect and relatively short orange-brown setae. The sensory setae are slightly spatulate, as in *S. saepium*, and subequal to the longest dorsal setae posterolaterally adjacent to the shield and on T2. Dorsal prominent

setae occur in groups of ca 20 on T2-A6 and are ca 2X as long as other dorsal and lateral setae on those segments (fig. 56a). Clavate dendritic setae occur on the prothoracic shield near the sensory setae and on A7. All other dorsal and lateral setae are tapered. The body is rather flat dorsally between the rows of dorsal prominent setae resulting in an angulate cross-section even more pronounced than in *S. sylvinus*.

Strymon

Larvae of the three *Strymon* species in California are very similar to each other and to larvae of *C. (Callophrys)* and *C. (Incisalia)*. They are covered with nonpigmented (except apically darkened), erect, straight, tapered setae; prominent setae on T2-A6 are absent or obscure (not much longer than surrounding setae) and dendritic setae are inconspicuous and confined to the margin of the honey gland. They differ from larvae of *Callophrys (Callophrys)* and *C. (Incisalia)* by their more filiform and less prominently spiculate sensory setae, smaller head, and by slight differences in cephalic pigmentation. Dark infuscation on the head is confined to an arc connecting ocelli 1-5 and extending posteriorly to ocellus 6 (figs. 65-67), whereas in *C. (Callophrys)* and *C. (Incisalia)* the cephalic infuscation is usually either more extensive (broadly encompassing all ocelli) or limited to ocelli 1-5. The ratio of the head width to the distance between insertions of the sensory setae on the prothoracic shield is usually at least 2.2 in both *S. avalona* and *S. melinus*, about 2.0 in *S. columella*, and usually less than 2.0 in *C. (Callophrys)* and *C. (Incisalia)*.

Strymon melinus occurs throughout the state and probably has the widest host range of any North American lycaenid. In California its larvae are most often found on *Eriogonum* (Polygonaceae) and various members of the Fabaceae and Malvaceae. *Strymon avalona* occurs only on Santa Catalina Island and utilizes *Eriogonum* (Polygonaceae) and *Lotus* (Fabaceae) (Gorelick, 1987). *Strymon columella*, largely subtropical in distribution, occurs in southern California and utilizes *Hibiscus, Sphaeralcea*, and other Malvaceae as larval hosts. The larvae of *S. columella* can be distinguished from those of *S. melinus* by the milky color of their chalazae; this character is best seen in live larvae. Other differences include a narrower host range and smaller distribution. The limited distribution of *S. avalona* may be the best clue to distinguish it from *S. melinus*; also, its head is slightly browner and the ocellar infuscation is a little darker and more extensive (fig. 65), but otherwise they are virtually indistinguishable.

Polyommatinae

All California members of this subfamily belong to the tribe Polyommatini. The head is about 1/4 as broad as the body and almost always black (but lighter brown in two local species and nonpigmented in many

exotic species); most species have a honey gland and eversible tubercles; the prothoracic shield is nonsclerotized, nonpigmented (although there may be dark chalazae), and often has a smoothly convex anterior margin; the bases of the sensory setae may appear sunken below the cuticular surface due to the height and density of cuticular ridges. The chalazae frequently appear stellate due to distolateral points. Prominent setae (at least subequal to the length of sensory setae) commonly occur on the prothoracic shield. The majority of species in this subfamily are univoltine and active in spring or summer, but some species and/or subspecies appear in late summer or fall; a few species are facultatively bi- or trivoltine while others are multivoltine.

Agriades

One species of this genus, *A. franklinii*, occurs in California usually above 3000m in the Cascade and Sierra Nevada Mts. but as low as 2000m in the Siskiyou Mts.; it is associated with wet meadows and boggy stream and lake margins. This species is partially bivoltine with diapause in the second instar. Eggs and larvae were found on *Dodecatheon alpinum* (Gray) Greene (Primulaceae) near Sonora Pass. The larvae mine the leaves until the last instar. This is the only polyommatine in California which lacks both a honey gland and eversible tubercles. Other distinguishing features include the dark brown color of setae (even ventrally), spiracles, and legs. Distinct dorsal and lateral prominent setae are present, and all setae are erect and straight to slightly curved; chalazae are distinctly stellate. The ground color is deep, bright green and there is a red middorsal line (fig. 74-7d).

Brephidium

One member of the genus *Brephidium, B. exilis*, is widespread in California. It is multivoltine and occurs commonly in relatively xeric and saline habitats where its major hosts, *Atriplex, Chenopodium*, and *Salsola* (Chenopodiaceae) thrive; *Sesuvium verrucosum* (Aizoaceae) is also used in some areas (Johnson, 1981). Larvae are various shades of green and usually without distinct markings (fig. 74-8a); often the body appears finely granular or pollinose. Prominent setae (2-3X as long as the spiracles) occur only along the anterior margin of T1, laterally on T2, and along the posterior margin of A9-10. All other dorsal and lateral setae are clavate-capitate, often bent parallel to the body surface, and ca as long as the spiracle width. All setae are nonpigmented and chalazae are weakly stellate. The sensory setae are finely tapered and at least twice as long as all other dorsal setae on T2-A8. Dendritic setae are absent.

Celastrina

One species, *C. argiolus*, occurs throughout California in many habitats but not in the desert lowlands. In California the larvae utilize

primarily *Ceanothus* (Rhamnaceae) and many hosts in the Rosaceae; they are rarely found on *Lotus* (Fabaceae) (Gorelick, 1987). In Arizona they also utilize *Amorpha (Fabaceae)* (Noel McFarland, personal communication) and *Eriogonum* (Polygonaceae). Larvae prefer to feed on flowers, buds, and immature fruit. Adults fly in spring and early summer throughout most of California and are partially bivoltine (at least in southern California) with pupal diapause. Most setae are bent parallel to the body surface and arise from strongly stellate chalazae (fig. 2f). The chalazae are crowded and their lateral points are often so long (the span between opposite points may be nearly as great as the setal length) that they may interdigitate; only *L. marina*, among other California species, approaches this condition. The sensory setae on the prothoracic shield are slightly expanded and flattened in the apical third (ca 2X as broad as the basal width) and are ca 3-4X as long as other setae on the shield; their length is subequal to a pair of prominent dorsal setae on T2 and ca 2-3X as long as all other dorsal setae on T2-A6. A few dendritic setae occur at the lateral margins of the honey gland and lateral to the sensory setae on the prothoracic shield. Larvae are polymorphic in coloration. The ground color is often whitish, pale pink or pale green; distinct lateral lines and chevrons are lacking but a conspicuously dark green, pink, or brownish transverse bar usually occurs on A1. A color morph common for larvae found on *Adenostoma fasciculatum* is illustrated in fig. 74-8b.

Euphilotes

The genus *Euphilotes* is extremely complex with four species and numerous subspecies in California. One member, *E. mojave*, is often considered a subspecies of *E. enoptes* (Pratt and Ballmer, 1987). All *Euphilotes* larvae feed on buds, blossoms, and seeds of *Eriogonum*. Several hosts may be used by one species, but most local populations use a single host and only rarely do sympatric species (and subspecies) share a host. All members of this genus diapause as pupae and are typically univoltine; some populations of *E. enoptes* are facultatively bi- or trivoltine (Pratt and Ballmer, 1987). Published reports of five larval instars in *E. enoptes bayensis* (Langston) and *E. e. smithi* (Mattoni) by Langston and Comstock (1966) and Arnold (1983), respectively, are probably erroneous since we have found only four instars in hundreds of rearings representing all four *Euphilotes* species. Larval ground color may be white, pink, yellow, or brownish; color pattern ranges from non-patterned to strongly marked with white, pink, yellow, and/or brown middorsal and lateral lines and lateral chevrons (fig. 74-8c). Distinguishing morphological features of this genus include apically spatulate sensory setae (fig. 13), a few dendritic setae at the lateral margins of the honey gland and usually near the A1 spiracles, moderately to weakly stellate chalazae, and a variable number of prominent setae on T2-A6 (sometimes absent).

Larvae of *E. rita* are perhaps the most distinctive of the genus. Paired dorsal prominences on T3-A6 are steeply peaked, creating a saw-toothed lateral profile, and each usually has at least one prominent seta, which may be directed posteromedially (fig. 57c). More prominent setae occur laterally on T2-A10 and dorsolaterally on T2 (and occasionally on other segments). The ground color is white or pink; markings may be absent but usually there are reddish lateral chevrons on T2-A6 and a transverse bar on A1 (fig. 74-8d). The head is dark brown and the legs are a little lighter. Most nonprominent setae are strongly curved and may be bent parallel to the body. The eversible tubercles arise from distinct but low prominences and are everted frequently as the larva crawls; this may be related to the fact that this is the most strongly myrmecophilic member of the genus. This species occurs along the desert slopes forming the southern and western borders of the Mojave Desert, the east slope of the Sierra Nevada and in some of the desert mountains. Host plants include *Eriogonum davidsonii, E. deflexum, E. heermannii, E. kearneyi, E. microthecum, E. plumatella, E. roseum*, and *E. wrightii*. Flight activity ranges from May to September for various populations.

Larvae of *E. mojave* are similar to those of *E. rita* in distribution of prominent setae. But segments T3-A6 are more rounded dorsally (fig. 57b); the eversible tubercles do not arise from dorsolateral prominences; and the legs, although brown, are much lighter than the head. Populations of *E. mojave* occur scattered through the Mojave Desert and desert slopes bordering it. Larvae can be found in spring on the annuals *E. pusillum* and *E. reniforme*.

Larvae of *E. battoides* and *E. enoptes* are best distinguished according to host plant and locality. In both species dorsal prominences are not apparent and dorsal prominent setae are usually absent posterior to T2 (fig. 57a); the legs are nonpigmented; the number of prominent setae in specific locations differs for different populations; and nonprominent setae are generally short and bent parallel to the body surface. *Euphilotes battoides* utilizes *E. fasciculatum* (everywhere), *E. parvifolium* (along the south coast), *E. heermannii* and *E. microthecum* (in the eastern Mojave Desert), and *E. umbellatum* and various cespitose *Eriogonum* species in the Cascade, Sierra Nevada, Siskiyou, and White Mountains. *Euphilotes enoptes* utilizes *E. nudum* everywhere north and west of the San Bernardino Mts., *E. elongatum, E. davidsonii*, and *E. wrightii* everywhere south and east of the San Gabriel Mts., *E. latifolium* and *E. parvifolium* along the central coast, and *E. elatum* and *E. umbellatum* in the Cascade, Sierra Nevada, and Siskiyou Mountains. Various populations of both species fly in spring, summer, or fall.

Everes

Two species of *Everes* occur in California; *E. amyntula* is widespread from sea level to over 3000m throughout the state (except low elevations

of the deserts), while *E. comyntas* occurs in mesic habitats generally below 1000m from the southern San Joaquin Valley northward. One distinctive feature easily separates this genus from all others in California; the spatulate lobes of the prolegs have sharply defined (somewhat scerotized and pigmented) lateral margins, especially basally (fig. 72b). This trait also occurs in *E. argiades* from Japan. The ground color is green, grey, or pinkish grey; a cream lateral line bordered with pink may be present. Both species are at least facultatively multivoltine with diapause in the last instar.

In California these species usually can be distinguished by setation differences, but some populations in the north and along the Sierra Nevada are intermediate. In larvae of *E. amyntula* dendritic setae are few in number and confined to the margin of the honey gland; other dorsal and lateral setae are erect and straight to slightly curved (rarely bent parallel to the body surface). In *E. comyntas* we found a few (ca 4) dendritic setae around the honey gland, and others near the A1 spiracles and occasionally laterally on T3; but Lawrence and Downey (1966) illustrate (in Illinois larvae) ten dendritic setae near the honey gland and report that others may occur near the A2 spiracles. Many dorsal and lateral setae in *E. comyntas* are curved or bent (often parallel to the body surface), especially on A7 and A8. In some (especially southern) populations of *E. amyntula* the eversible tubercles appear to be noneversible, although their location is marked by the usual wrinkled depression encircled by setae. This may be an adaptation to their habit of feeding only inside *Astragalus* seed pods where it is less likely that they would encounter ants. The larvae of *E. comyntas* and northern California populations of *E. amyntula* which commonly feed externally on various herbaceous Fabaceae have fully functional eversible tubercles.

Glaucopsyche

There are two species of *Glaucopsyche* in California; their larvae are often similar to those of *Lycaeides* and some *Icaricia* species. They are densely covered with short, tapered, nonpigmented setae; the sensory setae are finely tapered; chalazae are moderately stellate; and the dorsal setae on A7 and A8 (between the spiracles) are tapered and suberect to strongly recurved. Larvae of *G. piasus* have dendritic setae laterally on T3-A3, A6, and A7; there are 6-8 prominent dorsal setae anteriorly on T2 which are 2-3X as long as the spiracles and slightly longer than the sensory setae; all other dorsal and lateral setae on T1-A6 are erect, tapered, and .5-.75X as long as the spiracles. Larvae of *G. lygdamus* have dendritic setae around the A1 spiracles (also occasionally around the A2 spiracles and laterally on T3) and (less conspicuously) at the lateral margins of the honey gland. They also have 1-3 pairs of dorsal prominent setae on T2-A6 which are .5-1X as long as the sensory setae and 3-5X as long as the spiracles and other dorsal and lateral

setae. In cismontane southern California populations of *G. lygdamus*, nonprominent dorsal and lateral setae on T2-A6 are suberect to strongly curved (often bent parallel to the body); but in populations from northern California and east of the Sierra Nevada from the central Mojave Desert northward these setae are more erect (never bent parallel to the body). Larval coloration is polymorphic for *G. lygdamus*, ranging from concolorous green to pink and yellow with strong chevron markins and a well defined dorsal line (fig. 74-9a). Larvae of *G. piasus* are less polymorphic with a dull green or gray ground color and lateral chevrons (fig. 74-9b). Larvae of *G. piasus* feed only on lupine, while larvae of *G. lygdamus* utilize *Astragalus, Lotus, Lupinus* and *Vicia.* Both species are univoltine, have pupal diapause, and fly in spring or early summer.

Hemiargus

The two California species of *Hemiargus* are multivoltine and generally restricted to the southern and eastern regions. Their larvae greatly resemble those of the *Icaricia acmon* species group with which they share the following characters: finely tapered sensory setae, at least four prominent dorsal setae on T2 and at least two each on T3-A6, few dendritic setae at the lateral margins of the honey gland and occasionally near the A1 spiracles, and the majority of dorsal and lateral setae suberect to bent parallel to the body surface. However, the most strongly bent setae (near the abdominal spiracles and dorsally on A7 and A8) are somewhat spindle-shaped, flattened, and acutely pointed (fig. 21), whereas in the *I. acmon* species group, setae in the same areas are cylindric and apically blunt or truncate (fig. 2m).

Slight differences in setation distinguish these species. Larvae of *H. ceraunus* sometimes have a few dendritic setae near the A1 spiracles; also, the longest dorsal setae on T2 are no more than .75X as long as the longest setae on the prothoracic shield; and segments T3-A6 have one (or no) pair of dorsal prominent setae (fig. 58a). Larvae of *H. isola* lack dendritic setae near the A1 spiracles; the longest dorsal setae on T2 are at least as long as the longest setae on the prothoracic shield; and there are usually at least two pairs of prominent setae on T3-A6 (fig. 58b). Larvae of both species feed on members of the Fabaceae but larvae of *H. ceraunus* also utilize *Eriogonum* (Polygonaceae). The ground color may be green, red, brownish, or yellow; markings may be absent but often there is a reddish middorsal line and red or yellow lateral lines and dorsolateral chevrons (fig. 74-9c).

Icaricia

There are five species of *Icaricia* in California. They all have a few dendritic setae near the A1 spiracles and lateral margins of the honey gland, moderately stellate chalazae, and flagelliform sensory setae. The number and relative size of prominent setae on the prothoracic shield,

dorsally on T2-A6, laterally on all segments, and subdorsally on T2-A7 differs in each species. In all but *I. icarioides* the prominent dorsal setae are somewhat curved or inclined posteriorly. Other dorsal and lateral setae are tapered to blunt, erect to recurved and may be bent parallel to the body surface. Nondendritic dorsal setae on A7 and A8 are usually somewhat clavate and may be bent parallel to the body surface. *Icaricia acmon* is multivoltine and *I. neurona* is partially bi- or trivoltine; the other *Icaricia* species are univoltine. Diapause occurs in the egg for *I. shasta*, but in the second instar for the other species.

Three species (*I. acmon, I. lupini,* and *I. neurona*) constitute the *I. acmon* species group. Morphological differences in larvae of these species are slight; they are best distinguished according to host plant, locality, and season. The following character discussion is based on populations in the San Bernardino Mountains and does not necessarily apply to populations elsewhere. The length and abundance of prominent setae are generally greatest in *I. neurona* and least in *I. lupini*, thus affording some utility in species identification. Another distinguishing feature concerns the subdorsal prominent setae on A7 (ca midway between the honey gland and spiracles); in *I. neurona* these are well developed, while in *I. lupini* they are usually absent, and in *I. acmon* they are usually present but weakly differentiated from surrounding setae. Dorsal setae on A7 and A8 are semi-erect to strongly bent, (often parallel to the body) weakly tapered to clavate, and mostly apically blunt. Larval ground color is dark green in *I. lupini*, gray-green to dull pinkish gray in *I. neurona*, and highly variable (including green, cream, and maroon) in *I. acmon*. All three species may have a white or yellow lateral line, which in *I. acmon* may be bordered with red. The latter species may also have a contrastingly colored middorsal line and lateral chevrons.

Icaricia acmon, the most common and widespread species, occurs from early spring to fall in all habitats except the open desert; larvae feed on several species of *Eriogonum* and *Lotus*. *Icaricia lupini* is also widespread and utilizes *Eriogonum* as a larval host but is restricted to montane and foothill habitats; in southern California its host is *Eriogonum fasciculatum*, but elsewhere *E. umbellatum* is the major host. *Icaricia neurona* is restricted to montane habitats (usually above 2000m) from the southern Sierra Nevada to the San Bernardino Mountains; hosts are various cespitose *Eriogonum* species, especially *E. kennedyi* and *E. wrightii*.

Larvae of *I. shasta* are similar in appearance to larvae of the previous three species, but differ primarily in the greater development of prominent setae. They differ from all other *Icaricia* in having dark legs and dark chalazae on the prothoracic shield. The ground color is brown to maroon and there are yellowish dorsolateral chevrons and lateral lines (fig. 74-9d); the dorsolateral chevrons may be so enlarged that the ground color is reduced to a narrow line middorsally. They feed on

several cespitose *Astragalus* and *Lupinus* species mostly above 3000m in the Cascade, Sierra Nevada, Warner, and White Mountains.

Icaricia icarioides is a widespread species with various populations occupying habitats from sea level to over 3000m. Larvae feed on perennial lupines and range in ground color from green to pinkish grey. Larval setation differs substantially from that of the other *Icaricia* species; nearly all dorsal and lateral setae on T2-A6 are erect, acutely tapered, straight, and no longer than the spiracle width. Sensory setae are ca 4X as long as other setae on the prothoracic shield and slightly longer than the prominent dorsal setae on T2. Dorsal prominent setae on T3-A6 are no more than ca 1.5X as long as the spiracle width and may be weakly differentiated from other dorsal setae on those segments.

Leptotes

Only one species, *L. marina*, occurs in California. It is multivoltine and abundant throughout southern California, but less common in the Central Valley and uncommon or absent in the central and northern regions of the state. Larval hosts are primarily various Fabaceae and *Plumbago* (Plumbaginaceae), a common ornamental which probably accounts for the success of this species in urban areas; *Adenostoma fasciculatum* (Rosaceae) is also rarely used. The ground color is variable, ranging from pink to green and brownish violet. In general appearance the larvae appear most similar to those of *C. argiolus*. They have apically spatulate sensory setae and are covered with short erect setae arising from strongly stellate chalazae (the lateral points of adjacent chalazae may interdigitate) (fig. 2e); dorsal prominent setae occur on T2 and occasionally on other segments. Larvae of *L. marina* are uniquely distinguishable (among California lycaenids) by the presence of numerous broadly recurved and finely tapered setae (fig. 2b) dorsally and along the lateral fold, intermixed with shorter erect or only slightly bent setae. Similar recurved setae occur in *L. cassius* (Downey and Allyn, 1979) from Florida and in *Syntarucus plinius* from the Australasian region.

Lycaeides

Two species of *Lycaeides* occur in California. *Lycaeides melissa* ranges throughout the state (except the Colorado and Mojave deserts) from near sea level to over 3000m, while *L. idas* occurs primarily above 2000m in the Cascade, central and northern Sierra Nevada, Siskiyou, and Warner Mountains. Larval ground color is green (fig. 74-10a); although some larvae have whitish middorsal and lateral lines and dorsolateral chevrons, others are unmarked. Host plants are herbaceous Fabaceae including *Astragalus, Lotus*, and *Lupinus*. Lowland populations of *L. melissa* are multivoltine while montane populations above 2000m of both species are probably univoltine; diapause occurs as ova.

Physical distinctions between larvae of these species in California are subtle and they are best distinguished by locality. The sensory setae are tapered while dorsal and lateral prominent setae on T2-A6 are ca 3-4X as long as the spiracle width. Other dorsal and dorsolateral setae on T2-A6 are erect, ca as long as the spiracle width, tapered, and arise from moderately stellate chalazae. Typically they have 10-40 dendritic setae per segment near or in the latitude of the spiracles on T3-A2 and A6-A8; fewer dendritic setae may also be present laterally on T1 and T2. Other dorsal setae on A7 and A8 are erect and clavate-capitate, not strongly curved or bent.

Lycaeides larvae from near Mono Lake and the Warner Mountains differ from other populations examined. Their dendritic setae are difficult to observe since they are much smaller and number 0-8 per segment. Most nonprominent dorsal and subdorsal abdominal setae are truncate and sometimes peg-like; some, especially near the honey gland, may be sharply bent near the apex, resembling a railroad spike.

Philotes

There is one species of *Philotes, P. sonorensis*, which occurs throughout cismontane southern California (mostly below 2000m) and northward approximately to the latitude of San Francisco. This insect is univoltine with pupal diapause and flies in late winter and spring; larvae feed on *Dudleya* (Crassulaceae). Ground color ranges from pale green to pink and there are no contrasting markings (fig. 74-10b). Prominent dorsal setae occur only on T2; other dorsal and lateral setae on T2-A6 are erect, straight, weakly tapered to truncate, and ca .5-.7X as long as the spiracle width. Dendritic setae at the margins of the honey gland are clavate, longer than the spiracle width, and appear velvety due to numerous unusually short spicules (fig. 17). Other dorsal setae on A7 and A8 are clavate to strongly capitate (fig. 25) and mostly less than half as long as the spiracle width. The spiracles are brown and the proleg spatulate lobes are small and knob-like.

Philotiella

This genus is closely related to *Euphilotes* and contains a single species, *P. speciosa*, which is nearly confined to the southeastern desert areas of California. The rare subspecies, *P. s. bohartorum* (Shields), occurs in the western foothills of the Sierra Nevada. This species in univoltine with pupal diapause and flies in spring; larval hosts include *Eriogonum reniforme* and *Oxytheca*, especially *O. perfoliata* (Polygonaceae). The larval ground color is green or yellowish and there may be reddish middorsal and lateral lines and dorsolateral chevrons (fig. 74-10c). This species was long included in the genus *Philotes* along with all members of *Euphilotes*. The larvae of *P. speciosa* are most similar to those of *E. mojave* in general appearance; they differ in having virtually

nonstellate chalazae, lighter head pigmentation, and more erect setae. They also differ from larvae of all other California polyommatines except, *A. franklinii,* in lacking eversible tubercles.

Plebejus

There is one California species of *Plebejus, P. saepiolus*, which occurs generally above 2000m from Riverside County northward. It is univoltine with diapause in the second instar; larvae feed on *Trifolium* (Fabaceae). The larva is green and often has a white lateral line. In many respects the larvae of this species are similar to those of *Icaricia*. They differ in having dendritic setae on A7 extending from the honey gland laterally to the spiracles, whereas in *Icaricia* the dendritic setae on A7 are confined to the margin of the honey gland. They also differ from all *Icaricia* except, *I. shasta*, in having dark legs.

Plebulina

The single species of *Plebulina, P. emigdionis,* occurs only in a few scattered colonies in and around the western Mojave Desert. It is partially bi- or trivoltine and larvae feed on *Atriplex canescens* (Chenopodiaceae). This is the most distinctive California member of the Polyommatinae in terms of biology and larval morphology. It is the only one whose larvae lack a spatulate lobe on the prolegs, have more than four instars (5-7), and are restricted to a single host plant species. Also, the chalazae appear buttressed rather than stellate; but, unlike the buttressed chalazae of thecline larvae, the lateral ridges do not appear to be basally fused with the cuticle. Dendritic setae are few in number and confined to the vicinity of the A1 spiracles and margin of the honey gland; they and most other dorsal and lateral setae on T2-A6 are erect, tapered, and ca half as long as the spiracle width. A pair of prominent dorsal setae on T2 are ca 6X as long as the spiracle width. As with many other polyommatine larvae, most dorsal setae on A7 and A8 are clavate and strongly bent or recumbent. Lenticles are dark brown in contrast to most chalazae which are nonpigmented. The sensory setae are filiform. Larvae are grayish pink or green and lack contrasting markings (fig. 74-10d). They probably feed nocturnally; during the day they can be found at the base of the host plant in the company of ants.

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GLOSSARY

A1, A2, A3,. . . A10: Abdominal segments 1, 2, 3,. . . 10.

Adfrontal sutures: A pair of sutures extending dorsally from the anterior mandibular articulations and converging at the stem of the epicranial (or coronal) suture. In many Lepidoptera (but not Lycaenidae) two pairs of roughly parallel sutures extend from the coronal suture to the mandibular articulations, the more mesal frontal sutures and lateral to them the adfrontal sutures.

Allopatric: Occurring in different areas; usually pertaining to species or subspecies whose ranges do not overlap.

Anal: Pertaining to the last adbominal segment.

Anal prolegs: The terminal pair of prolegs on abdominal segment 10.

Biordinal: Two sizes, as in two lengths of crochets arising from a single line.

Bivoltine: Having two generations per year.

Buttressed chalazae: Chalazae with vertical lateral ridges which fuse distally with the cuticle, appearing buttressed (fig. 2n).

Ca: About or approximately.

Capitate: Abruptly enlarged distally, especially pertaining to setae.

Caudad: In the direction of the anal or tail end; posterior.

Cephalad: In the direction of the head; anterior.

Cephalic: Pertaining to the head.

Chaetotaxy: The arrangement or distribution of setae.

Chalaza(ae): A sclerotized basal papilla from which a seta arises.

Clavate: Club-shaped; more-or-less cylindric and gradually enlarged distally, especially pertaining to setae.

Coxa(ae): The basal segment of a true leg.

Crochet(s): A hooklike sclerotized structure at the distal end of a proleg, usually with many others arranged in rows.

Cylindric: Circular in cross-section, especially pertaining to setae.

Dendritic seta(ae): A specialized seta (usually) with relatively long, fine lateral spicules and often occurring in close proximity to the honey gland and spiracles (figs. 15-18).

Distal: Toward the end of an appendage farthest from its attachment.

Dorsal: Toward or pertaining to the dorsum.

Dorsal line: A longitudinal line along the dorsum, often apparent as a contrasting color with respect to the ground color.

Dorsum: The top of a larva when resting on a substrate; the side opposite its legs.

Echinoid seta(ae): Short globular setae with stout, apically flared processes found in *Calephelis* larvae (fig. 31).

Epicranial suture: A 'Y'-shaped suture separating left and right halves of the cranium which is forked anteriorly.

Eversible tubercle(s): A fleshy tubercle in many lycaenid larvae, located slightly posterolateral to the spiracle on abdominal segment 8, which is normally retracted and not visible.

Filiform: Filamentous or thread-like; slender, long, and little or not at all tapered, especially pertaining to setae.
Flagelliform: Whip-like; slender and finely tapered, especially pertaining to setae.
Frons: That portion of the head between the anterior arms of the epicranial suture (adfrontal or frontal sutures) and immediately above the clypeus.
Frontal sutures: The anterior arms of the epicranial suture which terminate at the anterior mandibular articulations and form the lateral margins of the frons. In lycaenid larvae these are also known as adfrontal sutures.
Ground color: The primary color of a larva on which a pattern of contrasting color(s) may be superimposed.
Honey gland: A partly eversible transverse middorsal gland on abdominal segment 7.
Instar: The stage between larval molts; the first instar emerges from an ovum; the last instar immediately precedes the pupal stage.
Lateral: Pertaining to the sides.
Lateral fold: A fleshy cuticular fold below the spiracles extending posteriorly from T1.
Lateral line: A longitudinal line of contrasting color coinciding with the lateral fold.
Lateral spicule: A small filamentous or spine-like lateral process of a seta.
Lenticle: A small cuticular lens-like structure, surmounting or set into a short chalaza-like collar, found in hesperiids and lycaenids.
Mesoseries: A band of crochets along the mesal side of a proleg.
Mesothorax: The second segment of the thorax, bearing the second pair true legs.
Metathorax: The third segment of the thorax, bearing the third pair of ture legs.
Middorsal: Located along the dorsal midline.
Multivoltine: Having several (continous) generations per year.
Mushroom lenticle: A stalked lenticle, narrowest at the base, found in *Atlides halesus* (fig. 26).
Mushroom seta(e): A short, stout, multibranched seta, resembling a mushroom when viewed under low magnification, found in the Lycaeninae (figs. 2q, 22).
Neck setae: Short, stout, tooth-like setae on the neck area of lycaenid larvae (fig. 27).
O1, O2, O3,. . .O6: Ocelli 1-6; numbered as in fig. 68.
Ocellus(i): One of six simple eyes or stemmata located on each side of the head of Lepidoptera larvae (fig. 68).
Onisciform: Somewhat spindle-shaped but ventrally flattened, as in the sow bug (*Oniscus*).
Papilla(ae): A small cuticular projection or elevation.

Pheromone: A chemical used by an organism to communicate with another member of its species.

Planta: The distal end of the proleg to which the crochets are attached.

Plumose seta(e): A type of seta (usually very long and filamentous) found in *Apodemia* and *Calephelis* larvae which has numerous short, fine lateral processes (figs. 31, 32).

Polymorphic: Having several forms or color patterns.

Posterior: Caudad.

Primary seta(e): Setae representing the archetypal setation of the Lepidoptera, occurring in fixed numbers and locations in many lepidopterous families but only in first instars of Lycaenidae.

Proleg: A fleshy appendage with distal crochets occurring in pairs ventrally on the abdominal segments.

Prominence: A fleshy elevation of the body surface.

Prominent seta(e): Setae occurring in locations typical for primary setae and which are distinguishable from surrounding secondary seta by their greater length and/or erectness; in some cases these may be primary setae but often they exceed the basic number of primary setae in a given location.

Pupa: The resting stage intermediate between the mature larva and adult in holometabolous insects.

Reclinate: Lying against or at a low angle to the body surface, especially pertaining to setae which are not bent near the base.

Recumbent: Lying down or reclining against the cuticle, especially pertaining to setae strongly bent near the base.

Recurved: Broadly bent back toward the base, especially pertaining to setae.

Retractile: Retractable; able to be withdrawn, as with the head of many lycaenid larvae.

Sclerite: A hardened (sclerotized) part of the body wall.

Secondary seta(e): Those setae occurring in addition to the basic complement of primary setae in larvae of lycaenids and many other lepidopterous families.

Semiochemical: Chemicals produced by one organism that incite response in other organisms.

Sensory seta(e): A specialized pair of setae located anterodorsal to the prothoracic spiracles; in lycaenid larvae they are on the prothoracic shield, near its lateral margins.

Seta(e): A sclerotized hair or bristle surrounded basally by a small cuticular ring and often arising from a chalazae.

Spatulate: Enlarged and compressed or flattened distally, as in a spatula, especially pertaining to setae.

Spatulate lobe: A fleshy lobe (usually distally flared and flattened) arising near the center of the mesoseries of crochets on most lycaenid larvae.

Spicule: A spine-like projection.

Spinule: A short sclerotized cuticular projection.

Spiracle: A sclerotized, cuticular pore associated with internal tracheae, a pair of which are located laterally on the prothorax and abdominal segments 1-8.

Stellate chalaza: A chalaza with distal or lateral pointed projections.

Stemma(ta): One of a group of lateral ocelli found in lepidopterous larvae; ocellus.

Subdorsal: Located slightly lateral to the dorsal midline, intermediate between the dorsal and lateral regions.

Subprimary seta(e): Those setae (additional to primary setae) occurring in fixed locations typical of some families.

Suture: A seam where two sclerites join.

Sympatric: Occurring in the same area.

T1, T2, T3: Referring to the prothorax, mesothorax, and metathorax, respectively.

Tapered: Becoming gradually narrower distally, especially pertaining to setae.

Triordinal: Pertaining to crochets of three lengths arising from a single row.

Taxon(a): A taxonomic unit such as species, genus, family, etc.

Uniordinal: Pertaining to crochets of a single length arising from a single line.

Ventral: Pertaining to the lower side of a larva when resting on the substrate; the side from which the legs and prolegs arise.

Ventral prothoracic gland: An eversible gland arising midventrally anterior to the prothoracic legs of some Lepidoptera larvae.

Verruca(e): A distinctly bounded (often sclerotized, pigmented, or raised) area from which several setae arise.

Appendix 1. List of the Lycaenidae of California

Riodininiae:
Apodemia mormo (C. and R. Felder, 1859)
" *palmerii* (W. H. Edwards, 1870)
Calephelis nemesis (W. H. Edwards, 1871)
" *wrighti* Holland, 1930
Lycaeninae:
Lycaena arota (Boisduval, 1852)
" *cupreus* (W. H. Edwards, 1870)
" *editha* (Mead, 1878)
" *gorgon* (Boisduval, 1852)
" *helloides* (Boisduval, 1852)
" *hermes* (W. H. Edwards, 1870)
" *heteronea* (Boisduval, 1852)
" *mariposa* (Reakirt, 1866)
" *nivalis* (Boisduval, 1869)
" *phlaeas* (Linnaeus, 1761)
" *rubidus* (Behr, 1866)
" *xanthoides* (Boisduval, 1852)
Theclinae:
Atlides halesus (Cramer, 1777)
Callophrys (Callophrys) comstocki Henne, 1940
" " *dumetorum* (Boisduval, 1852)
" " *lemberti* Tilden, 1963
" " *perplexa* Barnes and Benjamin, 1923
" *(Incisalia)* *augustus* (W. Kirby, 1837)
" " *eryphon* (Boisduval, 1852)
" " *fotis* (Strecker, 1878)
" " *mossii* (Hy. Edwards, 1881)
" (Mitoura) *johnsoni* (Skinner, 1904)
" " *loki* (Skinner, 1907)
" " *nelsoni* (Boisduval, 1869)
" " *siva* (W. H. Edwards, 1874)
" " *spinetorum* (Hewitson, 1867)
" " *thornei* (Brown, 1983)
Habrodais grunus (Boisduval, 1852)
Harkenclenus titus (Fabricius, 1793)
Ministrymon leda (W. H. Edwards, 1882)
Satyrium auretorum (Boisduval, 1852)
Satyrium behrii (W. H. Edwards, 1870)
" *californica* (W. H. Edwards, 1862)
" *fuliginosum* (W. H. Edwards, 1861)
" *saepium* (Boisduval, 1852)
" *sylvinus* (Boisduval, 1852)
" *tetra* (W. H. Edwards, 1870)
Strymon avalona (W. G. Wright, 1905)
" *columella* (Fabricius, 1793)
" *melinus* Hübner, 1818

Polyommatinae:

Agriades franklinii (Curtis, 1835)
Brephidium exilis (Boisduval, 1852)
Celastrina argiolus (Linnaeus, 1758)
Everes amyntula (Boisduval, 1852)
" *comyntas* (Godart, 1824)
Euphilotes battoides (Behr, 1867)
" *enoptes* (Boisduval, 1852)
" *mojave* (Watson and W. P. Comstock, 1920)
" *rita* (Barnes and McDunnough, 1916)
Glaucopsyche lygdamus (Doubleday, 1841)
" *piasus* (Boisduval, 1852)
Hemiargus ceraunus (Fabricius, 1793)
" *isola* (Reakirt, 1866)
Icarica acmon (Westwood and Hewitson, 1852)
" *icarioides* (Boisduval, 1852)
" *lupini* (Boisduval, 1869)
" *neurona* (Skinner, 1902)
" *shasta* (W. H. Edwards, 1862)
Leptotes marina (Reakirt, 1860)
Lycaeides idas (Linnaeus, 1761)
" *melissa* (W. H. Edwards, 1873)
Philotes sonorensis (C. and R. Felder, 1865)
Philotiella speciosa (Hy. Edwards, 1867)
Plebejus saepiolus (Boisduval, 1852)
Plebulina emigdionis (F. Grinnell, 1905)

Appendix 2. New and reconfirmed larval host plants.

Host species	Butterfly species
AIZOACEAE	
Sesuvium verrucosum Raf.	*B. exilis*
ASTERACEAE	
Baccharis glutinosa Pers.	*C. nemesis, C. argiolus*
Bebbia juncea (Benth.) Greene	*C. wrighti*
Helianthus annuus L. ssp. *lenticularis* *(Dougl.)* Ckll.	*S. melinus*
CHENOPODIACEAE	
Atriplex canescens (Pursh) Nutt.	*B. exilis, P. emigdionis*
" *semibaccata* R. Br.	*B. exilis*
Chenopodium sp.	*B. exilis*
Salsola iberica Sennen & Pau.	*B. exilis*
Suaeda moquinii (Torr.) Greene	*B. exilis*
CONVOLVULACEAE	
Cuscuta sp.	*C. (I.) augustus*
CRASSULACEAE	
Dudleya abramsii Rose	*P. sonorensis*
" *cymosa* (Lem.) Britt. & Rose	*P. sonorensis*
" *lanceolata* (Nutt.) Britt. & Rose	*P. sonorensis, S. melinus*
" *saxosa* (Jones) Britt. & Rose	*P. sonorensis, S. melinus*
Sedum spathulifolium Hook.	*C. (I.) mossii*
CUPRESSACEAE	
Juniperus californica Carr.	*C. (M.) loki, C. (M.) siva*
ERICACEAE	
Vaccinium arbuscula (Gray) Merriam	*L. mariposa*
" *myrtillus* L.	*L. mariposa* (Oregon record)
FABACEAE	
Amorpha californica Nutt.	*L. marina, S. melinus*
" *fruticosa* L. var. *occidentalis* (Abrams) Kearn. & Peeb.	*L. marina*
Astragalus canadensis L. var. *brevidens* (Gand.) Barneby	*L. melissa*
" *douglasii* (T. & G.) Gray	*E. amyntula, H. ceraunus, L. melissa*
" *lentiginosus* Dougl.	*E. amyntula, G. lygdamus, L. melissa*
" *palmeri* Gray	*E. amyntula, H. ceraunus*
" *whitneyi* Gray	*E. amyntula*
Calliandra eriophylla Benth.	*L. marina*
Dalea searalsiae (Gray) Barneby	*H. isola*

Hoffmannseggia microphylla Torr.	*H. ceraunus*
Lotus argophyllus (Gray) Greene	*S. avalona, C. perplexa*
" *crassifolius* (Benth.) Greene	*C. perplexa, S. melinus*
" *humistratus* Greene	*G. lygdamus* (Oregon record)
" *nevadensis* Greene	*I. acmon*
" *oblongifolius* (Benth.) Green	*L. idas*
" *purshianus* (Benth.) Clem. & Clem.	*I. acmon, L. melissa*
" *procumbens* (Greene) Greene	*G. lygdamus, L. marina*
" *rigidus* (Benth.) Greene	*G. lygdamus*
" *scoparius* (Nutt. in T. & C.) Ottley	*C. perplexa, G. lgydamus, L. marina, S melinus*
Lupinus andersonii Wats.	*G. piasus, S. fuliginosum*
" *argenteus* Pursh var. *tenellus* (Dougl. ex D. Don) D. Dunn	*I. icarioides*
" *breweri* Gray	*I. shasta*
" *caudatus* Kell.	*G. lygdamus, S. fuliginosum*
" *excubitus* Jones	*G. piasus, I. icarioides,*
" *latifolius* Agardh	*G. lygdamus, G. piasus, I. acmon, S. melinus*
" *magnificus* Jones	*H. isola*
Marina parryi (T. & G.) Barneby	*H. isola*
Medicago sativa L.	*L. marina*
Prosopis glandulosa Torr.	*H. ceraunus, L. marina, M. leda*
" *pubescens* Benth.	*A. palmerii*
Trifolium monanthum Gray	*P. saepiolus*
" *monoense* Greene	*P. saepiolus*
" sp.	*P. saepiolus*
Vicia benghalensis L.	*G. lygdamus*
FAGACEAE	
Quercus chrysolepis Liebm.	*H. grunus, S. auretorum*
" *cornelius-mulleri* Nixon & Steele	*S. auretorum*
" *douglasii* H. & A.	*S. auretorum*
" *wislizenii* A. DC.	*S. auretorum, S. californica*
LAMIACEAE	
Rosmarinus officionalis L.	*S. melinus*
Mentha piperita L.	*S. melinus*
MALVACEAE	
Gossypium hirsutum L.	*S. melinus*
Hibiscus denudatus Benth.	*S. columella, S. melinus*
" *rosa-sinensis* L.	*S. melinus*
Sphaeralcea emoryi Torr. in Gray	*S. melinus*
PLUMBAGINACEAE	
Plumbago auriculata Lam.	*L. marina*

POLYGONACEAE

Eriogonum caespitosum Nutt.	*I. lupini*
" *cinereum* Benth.	*E. battoides*
" *davidsonii* Greene	*E. enoptes, E. rita, H. ceraunus, I. acmon, S. melinus*
" *deserticola* S. Wats.	*A. mormo*
" *elatum* Dougl. ex Benth.	*E. enoptes, S. melinus*
" *elongatum* Benth.	*C. perplexa, E. enoptes, H. ceraunus, I. acmon, L. gorgon, S. melinus*
" *fasciculatum* Benth.	*A. mormo, C. comstocki, E. battoides, I. acmon, I. lupini, L. heteronea*
" *heermannii* Dur. & Hilg.	*A. mormo, C. comstocki, E. battoides*
" *heracleoides* Nutt.	*C. lemberti*
" *incanum* Torr. & Gray.	*E. battoides, C. lemberti*
" *inflatum* Torr. & Frem.	*A. mormo, S. melinus*
" *insigne* Wats.	*A. mormo*
" *kennedyi* Porter ex Wats.	*C. comstocki, E. battoides, E. enoptes, I. acmon, I. neurona*
" *latifolium* Sm.	*A. mormo, C. dumetorum, E. enoptes*
" *lobbii* T. & G.	*E. battoides, I. lupini*
" *marifolium* T. & G.	*C. lemberti, E. battoides*
" *microthecum* Nutt.	*C. comstocki, E. battoides, E. rita, S. melinus*
" *nidularium* Cov.	*C. comstocki*
" *nudum* Dougl. ex Benth.	*A. mormo, C. lemberti, E. enoptes, I. acmon, L. gorgon, S. melinus*
" *ovalifolium* Nutt.	*E. battoides, I. acmon, I. lupini*
" *panamintense* Morton	*E. enoptes*
" *parvifolium* Sm. in Rees	*E. battoides, E. enoptes, I. acmon, S. melinus*
" *plumatella* Dur. & Hilg.	*E. enoptes, E. rita, I. acmon, H. ceraunus*
" *pusillum* T. & G.	*E. mojave*
" *reniforme* Torr. & Frem.	*E. mojave, H. ceraunus, I. acmon, P. speciosa*
" *roseum* Dur. & Hilg.	*E. enoptes, E. rita, S. melinus*
" *thurberi* Torr.	*I. acmon*
" *umbellatum* Torr.	*A. mormo, C. comstocki, C. lemberti, E. battoides, E. enoptes, I. lupini, I. neurona, L. heteronea*
" *wrightii* Torr. ex Benth.	*C. argiolus (Arizona record), E. enoptes, H. ceraunus, I. acmon, S. melinus*

Oxyria digyna (L.) Hill	*L. phlaeas*
Oxytheca perfoliata T. & G.	*A. mormo*
Polygonum amphibeum L.	*L. hellodies*
" *lapathifolium* L.	*S. melinus*
Rumex angiocarpus Murbeck	*L. editha*
" *californicus* Rech.	*L. cupreus*
" *crispus* L.	*L. xanthoides*
" *paucifolius* Nutt. ex Wats.	*L. cupreus, L. editha*
" *salicifolius* Weinm.	*L. editha, L. xanthoides*
" *triangulivalvis* (Danser) Rech.	*L. cupreus, L. rubidus*
PRIMULACEAE	
Dodecatheon alpinum (Gray) Greene	*A. franklinii*
RHAMNACEAE	
Ceanothus cordulatus Kell.	*S. californica, S. saepium*
" *cuneatus* (Hook.) Nutt.	*S. saepium*
" *crassifolius* Torr.	*S. saepium*
" *greggii* Gray var. *perplexans* (Trel.) Jeps.	*C. (I.) augustus, S. saepium*
" *leucodermis* Greene	*C. (I.) augustus, C. argiolus, S. saepium*
" *oliganthus* Nutt. in T. & G.	*S. saepium*
" *palmeri* Trel.	*C. (I.) augustus, C. argiolus*
Rhamnus crocea Nutt. in T. & G.	*C. (I.) augustus, L. hermes*
" *ilicifolia* Kell.	*C. (I) augustus*
ROSACEAE	
Adenostoma fasciculatum H. & A.	*C. argiolus, C. (I.) augustus, L. marina*
Cercocarpus betuloides Nutt. ex T. & G.	*S. tetra*
Cowania mexicana D. Don var. *stansburiana* (Torr.) Jeps.	*C. (I.) fotis*
Heteromeles arbutifolia M. Roem.	*C. argiolus, C. (I.) augustus*
Malus sylvestris (L.) P. Mill.	*S. melinus*
Prunus ilicifolia (Nutt.) Walp.	*C. argiolus, C. (I.) augustus*
Purshia glandulosa Curran	*S. behrii*
" *tridentata* (Pursh) DC.	*S. behrii*
Rubus ursinus Cham. & Schlecht.	*S. melinus*
SALICACEAE	
Salix sp.	*S. melinus*
" *hindsiana* Benth.	*S. sylvinus, S. melinus*
" *lasiolepis* Benth.	*S. sylvinus*
SAXIFRAGACEAE	
Ribes quercetorum Greene	*L. arota*
" *roezlii* Regel.	*L. arota*
" *velutinum* Greene	*L. arota*

VISCACEAE

Arceuthobium campylopodum Engelm. in Gray	*C.(M.) spinetorum*
Phoradendron tomentosum (Englm. ex Gray)	*A. halesus*

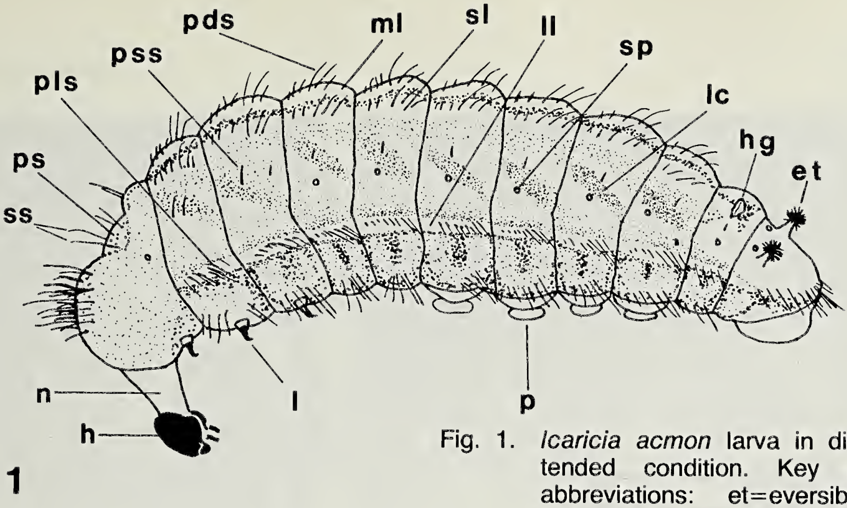


Fig. 1. *Icaricia acmon* larva in distended condition. Key to abbreviations: et=eversible tubercle, h=head, hg=honey gland, l=leg, lc=lateral chevron, ll=lateral line, ml=middorsal line, n=neck, p=proleg, pds=prominent dorsal setae, pls=prominent lateral setae, ps=prothoracic shield, pss=prominent subdorsal setae, sl=subdorsal line, sp=spiracle, ss=sensory setae.

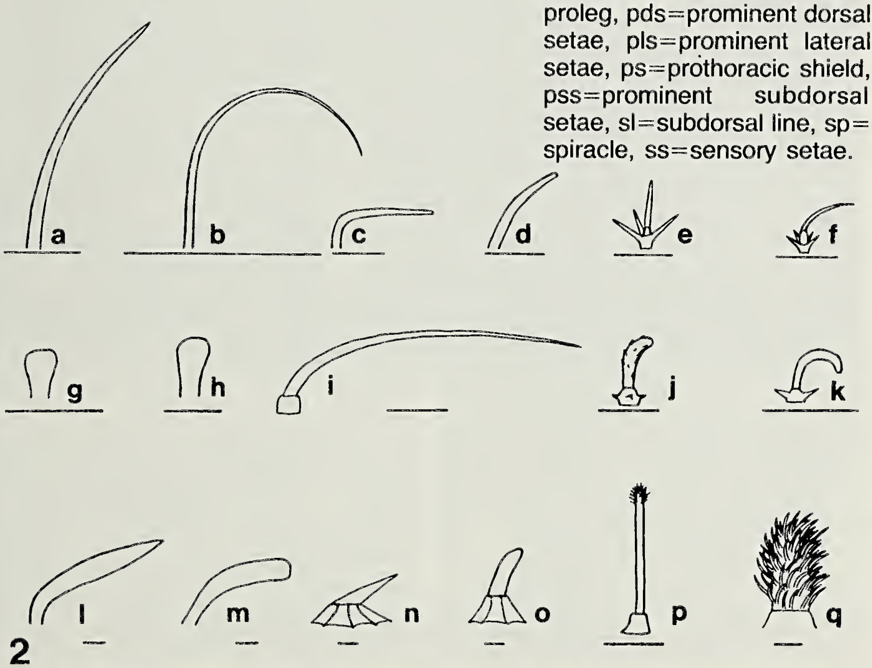
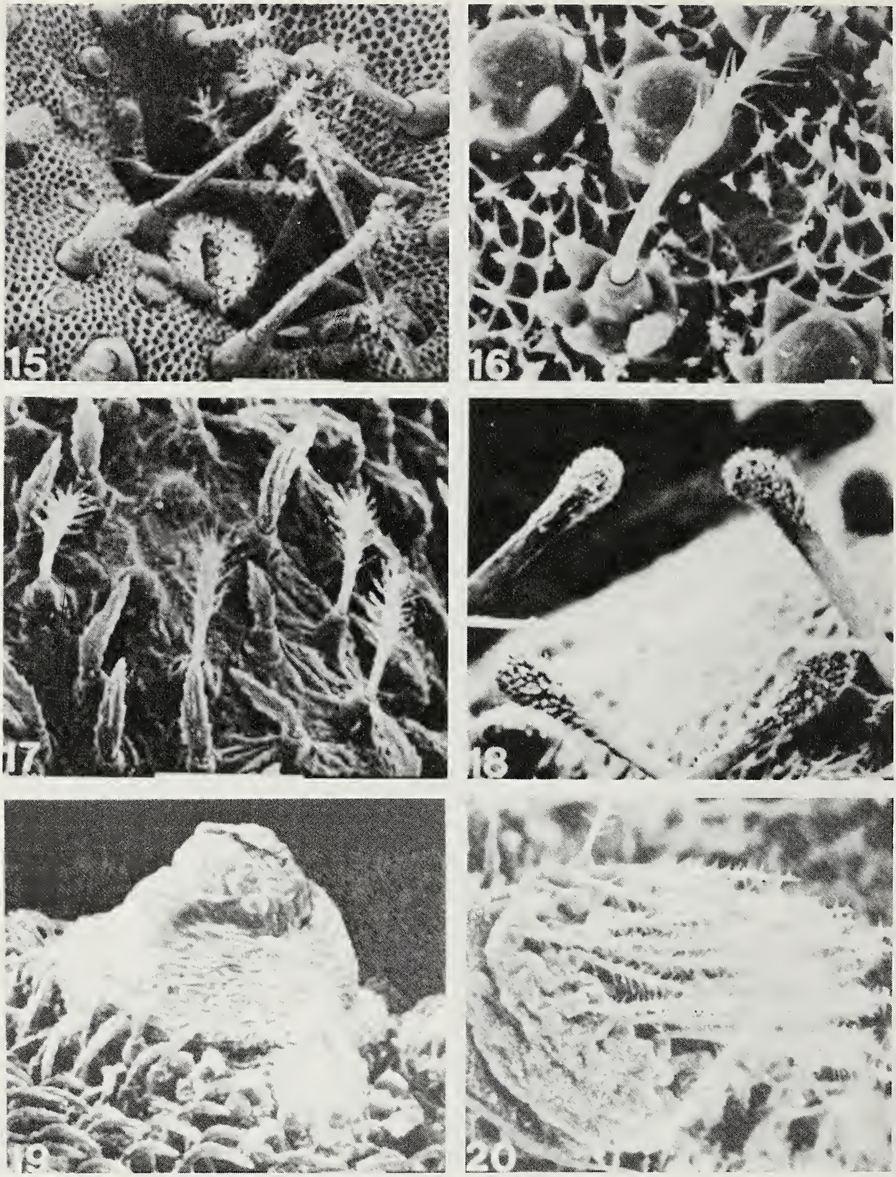


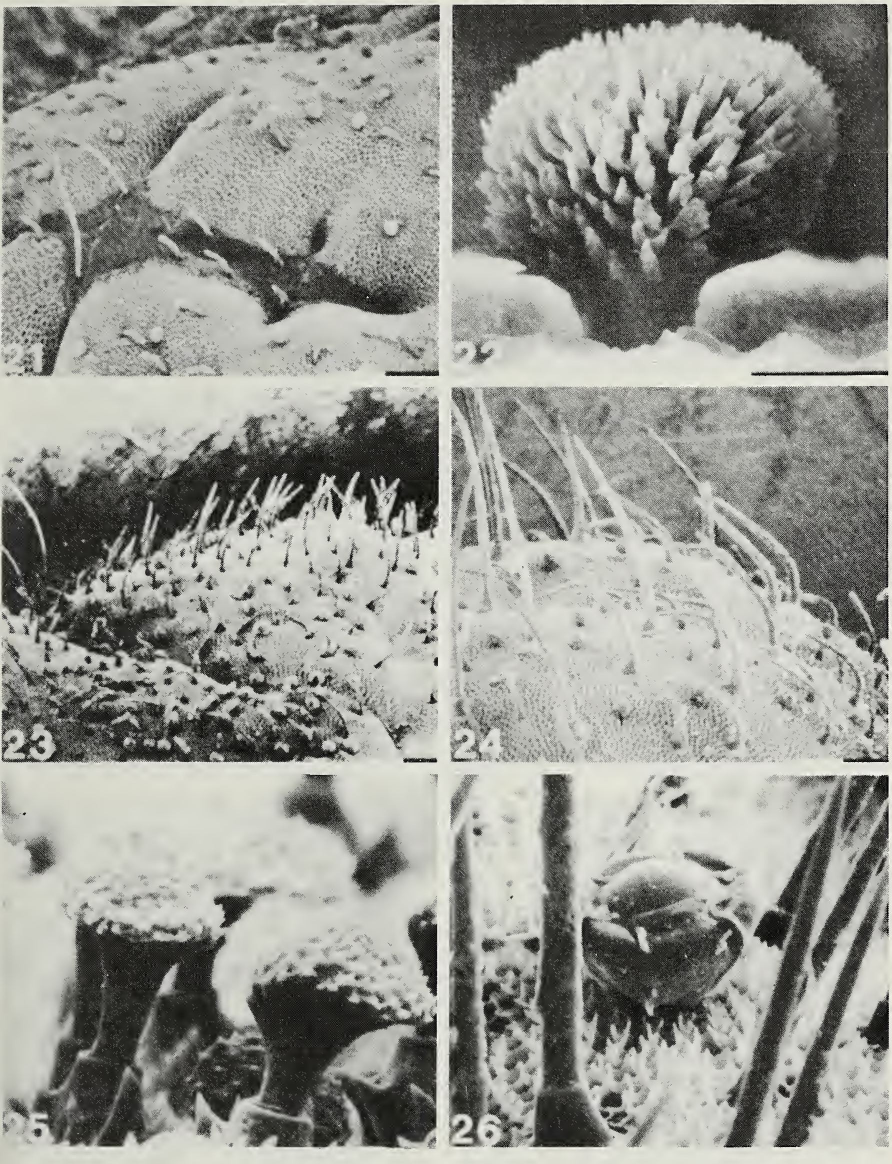
Fig. 2. Some variations in lycaenid setal structure: a) erect, slightly curved prominent seta (*L. nivalis*), b) broadly recurved and finely tapered seta (*L. marina*), c) seta sharply bent near base and apically truncate (*L. nivalis*), d) semierect, apically truncate seta (*L. mariposa*), e) erect, straight seta with stellate chalaza (*L. marina*), f) recurved, apically pointed seta with stellate chalaza (*C. argiolus*), g) clavate-capitate seta (*H. titus*), h) clavate-capitate seta (*L. xanthoides*), i) slender recumbent seta (*L. gorgon*), j) erect, apically bent seta with stellate chalaza (*L. melissa*), k) recurved, apically blunt seta with stellate chalaza (*G. piasus*), l) spindle-shaped, apically pointed seta (*H. ceraunus*), m) clavate, truncate seta (*I. acmon*), n) reclinate seta with buttressed chalaza (S. california), o) slightly inclined, blunt seta with buttressed chalaza (*S. fuliginosum*), p) weakly dendritic seta with nonsculptured chalaza (*L. heteronea*), q) mushroom seta with tapered, unbranched processes (*L. arota*). Bar scale=0.1mm for a-k and p and 0.01mm for l-o and q.

Figs. 3-8. Some head and body setae. Fig. 3. *Philotiella speciosa* head. Fig. 4. Prominent seta and other setae on mesothoracic dorsal prominence of *Callophrys (M.) johnsoni*. Fig. 5. *Apodemia mormo* head; note long setae on cranium and anterior margin of prothorax. Fig. 6. Branched sensory seta on *Atlides halesus*. Fig. 7. Lateral view of prothoracic dorsum of *Callophrys (C.) perplexa*. Note relatively low dorsal prominence posterolateral to the prothoracic shield with transverse row of prominent setae. Fig. 8. Lateral view of prothoracic dorsum of *C. (Mitoura) loki*. Note relatively high dorsal prominence posterolateral to the prothoracic shield lacking transverse row of prominent setae. Scale bar=0.1mm for figs. 3-6 and 1.0mm for figs. 7 and 8.

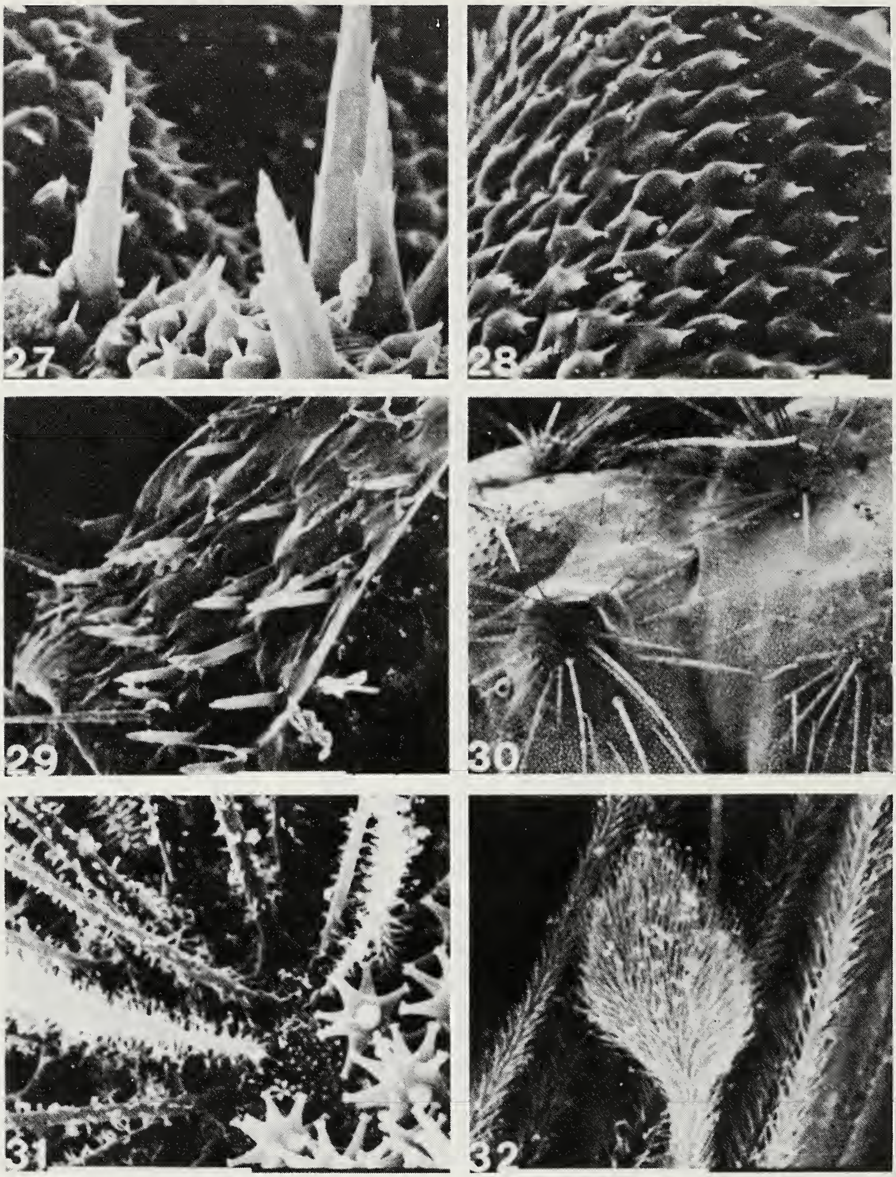
Figs. 9-14. Sensory setae on prothoracic shield. Fig. 9. *Callophrys (M.) loki*. Fig. 10. *Plebulina emigdionis*. Fig. 11. *Apodemia mormo*. Fig. 12. *Callophrys (M.) spinetorum*. Fig. 13. *Euphilotes mojave*. Fig. 14. *Lycaena xanthoides*. Scale bar=0.1mm.



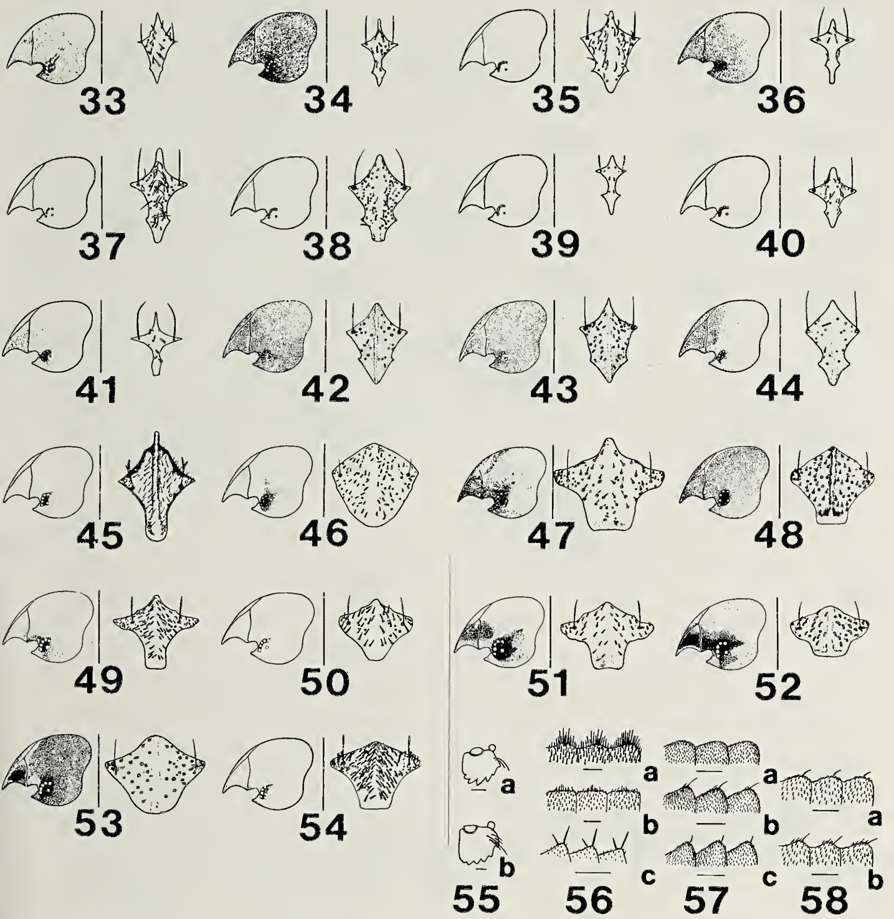
Figs. 15-20. Dendritic setae, eversible tubercle, and honey gland. Fig. 15. Dendritic setae around A7 spiracle of *Lycaena xanthoides*; note lenticles, clavate-capitate setae, and mushroom setae. Fig. 16. Dendritic seta near A1 spiracle on *Celastrina argiolus*; note stellate chalaza and lenticles. Fig. 17. Dorsolateral dendritic setae on mesothorax of *Satyrium behrii*; note strongly dentate setae bent parallel to body surface. Fig. 18. Dendritic setae near honey gland of *Philotes sonorensis* (silk fiber across center). Fig. 19. Everted honey gland of *Euphilotes battoides*. Fig. 20. Partially everted eversible tubercle of *Celastrina argiolus*; note strongly spiculate setae at apex. Scale bar=0.01mm for figs. 16 and 18 and 0.1mm for all other figs.



Figs. 21-26. Fig. 20. *Lycaena hermes* prothoracic shield. Fig. 22. Mushroom seta of *Lycaena xanthoides*. Fig. 23. Lateral view of setae posterolateral to the prothoracic shield of *Lycaena arota*; note most setae directed caudad. Fig. 24. Lateral view of setae posterolateral to the prothoracic shield of *Lycaena nivalis*; note setae directed cephalad. Fig. 25. Capitate setae near honey gland of *Philotes sonorensis*. Fig. 26. Mushroom lenticle of *Atlides halesus*. Scale bar=0.1mm for figs. 21, 23, and 24 and 0.01mm for figs. 22, 25, and 26.



Figs. 27-32. Various setae and spinules. Fig. 27. Neck setae and spinules of *Callophrys (M.) johnsoni*. Fig. 28. Spinules on neck of *Plebulina emigdionis*. Fig. 29. Setae on the frons of *Callophrys (I.) mossii*. Fig. 30. Lateral view of abdominal segments one and two of *Apodemia mormo*; note A1 spiracle anteroventral to lateral verruca. Fig. 31. Dorsal verruca of *Calephelis nemesis*; note echinoid (lower right) and plumose setae. Fig. 32. Spatulate tip of plumose seta of *Calephelis nemesis*. Scale bar=0.01mm for figs. 27, 28, and 32 and 0.1mm for figs. 29-31.

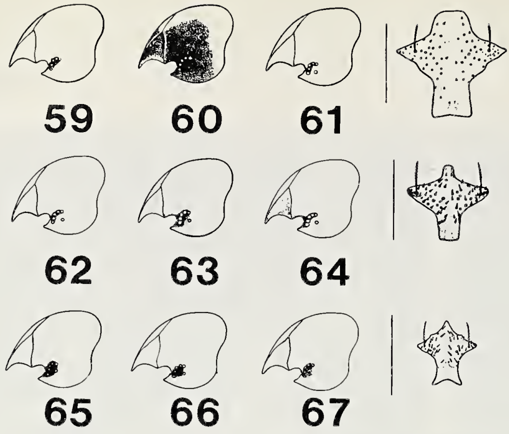


Figs. 33-44. Cranial pigmentation (left) and prothoracic shields (right) for 12 *Lycaena* species. Fig. 33. *L. phlaeas*. Fig. 34. *L. cupreus*. Fig. 35. *L. arota*. Fig. 36. *L. nivalis*. Fig. 37. *L. gorgon*. Fig. 38. *L. heteronea*. Fig. 39. *L. hermes*. Fig. 40. *L. helloides*. Fig. 41. *L. mariposa*. Fig. 42. *L. editha*. Fig. 43. *L. rubidus*. Fig. 44. *L. xanthoides*. Scale bar=1mm for prothoracic shield; crania not drawn to scale.

Figs. 45-54. Cranial pigmentation (left) and prothoracic shields (right) of *Atlides, Habrodais, Harkenclenus*, and *Satyrium* species. Fig. 45. *A. halesus*. Fig. 46. *H. grunus*. Fig. 47. *H. titus*. Fig. 48. *S. fuliginosum*. Fig. 49. *S. saepium*. Fig. 50. *S. sylvinus*. Fig. 51. *S. auretorum*. Fig. 52. *S. behrii*. Fig. 53. *S. californica*. Fig. 54. *S. tetra*. Scale bar=1mm for prothoracic shields; crania not drawn to scale.

Fig. 55. Mandibular setation of *Satyrium saepium* and *Lycaena xanthoides*, aboral surface of left mandibles. Fig. 55a. *S. saepium*. Fig. 55b. *L. xanthoides*. Scale bar=0.1mm.

Fig. 56-58. Dorsal profile and setae of abdominal segments 1-3 of *Satyrium tetra, S. auretorum, Ministrymon leda, Euphilotes enoptes, E. mojave, E. rita, Hemiargus ceraunus,* and *H. isola*. Fig. 56a. *S. tetra*. Fig. 56b. *S. auretorum*. Fig. 56c. *M. leda*. Fig. 57a. *E. enoptes*. Fig. 57b. *E. mojave*. Fig. 57c. *E. rita*. Fig. 58a. *H. ceraunus*. Fig. 58b. *H. isola*. Scale bar=1mm.



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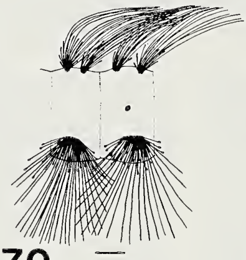

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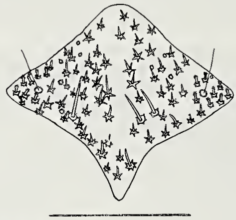

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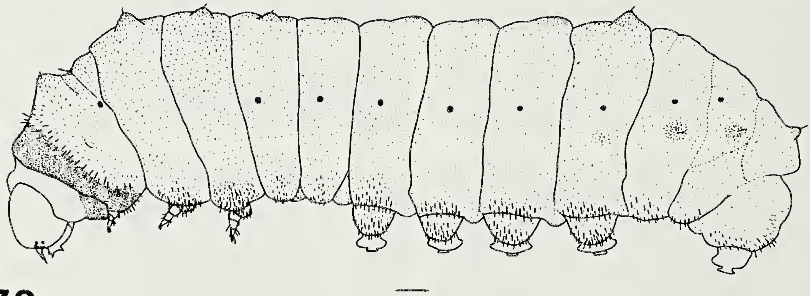

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Figs. 59-67. Cranial pigmentation and prothoracic shields of some *Callophrys* and *Strymon* species. Fig. 59. *C. perplexa* cranium. Fig. 60. *C. comstocki* cranium. Fig. 61. *C. (Mitoura) spinetorum* cranium (left) and prothoracic shield (right). Fig. 62. *C. (Incisalia) augustus* cranium. Fig. 63. *C. (I.) fotis* cranium. Fig. 64. *C. (I.) mossii* cranium (left) and prothoracic shield (right). Fig. 65. *S. avalona* cranium. Fig. 66. *S. columella* cranium. Fig. 67. *S. melinus* cranium (left) and prothoracic shield (right). Scale bar=1mm for prothoracic shields; crania not drawn to scale.

Fig. 68. *Lycaena xanthoides* ocelli; ocelli are numbered counterclockwise from the top. Scale bar=1mm.

Figs. 69, 70. Lateral view of abdominal segments 1 and 2 of *Apodemia mormo* and *Calephelis nemesis* showing placement of spiracles and verrucae. Fig. 69. *A. mormo*. Fig. 70. *C. nemesis*. Scale bar=1mm.

Fig. 71. Prothoracic shield of *Icaricia lupini*. Scale bar=1mm.

Fig. 72. Planta of prolegs of *Habrodais grunus* and *Everes amyntula*. Fig. 72a. *H. grunus*; note short series of lateral crochets. Fig. 72b. *E. amyntula*; note pigmented basal margins of spatulate lobe. Scale bar=0.5mm.

Fig. 73. Distended last instar *Callophrys (Mitoura) spinetorum* larva. Note prominent setae confined to dorsal and lateral prominences, other setae very short and sparse. Scale bar=1mm.

Fig. 74. Larval photographs of 40 lycaenid species. Species are listed from left to right(a-d) by row (1-10) from the top. Row 1: a) *A. mormo*, b) *A. palmerii*, c) *C. nemesis*, d) *L. arota*; row 2: a) *L. gorgon*, b) *L. hermes*, c) *L. heteronea*, d) *L. mariposa*; row 3: a) *L. nivalis*, b) *L. phlaeas*, c) *L. xanthoides*, d)*H. grunus*; row 4: a) *A. halesus*, b) *C. (C.) dumetorum*, c) *C. (C.) perplexa*, d) *C. (I.) augustus*; row 5: a) *C. (I). eryphon*, b) *C. (M.) nelsoni*, c) *C. (M.) spinetorum*, d) *H. titus*; row 6: a) *M. leda*, b) *S. auretorum*, c) *S. behrii*, d) *S. californica*; row 7: a) *S. fuliginosum*, b) *S. sylvinus*, c) *S. tetra*, d) *A. franklinii*; row 8: a) *B. exilis*, b) *C. argiolus*, c) *E. battoides*, d) *E. rita*; row 9: a) *G. lygdamus*, b) *G. piasus*, c) *H. isola*, d) *I. shasta*; row 10: a) *L. melissa*, b) *P. sonorensis*, c) *P. speciosa*, d) *P. emigdionis*. All subjects greater than life size. Orientation is standard (cephalad at left) except 1d, 2d, 5a, 7b, 8c, and 9d with cephalad at right.

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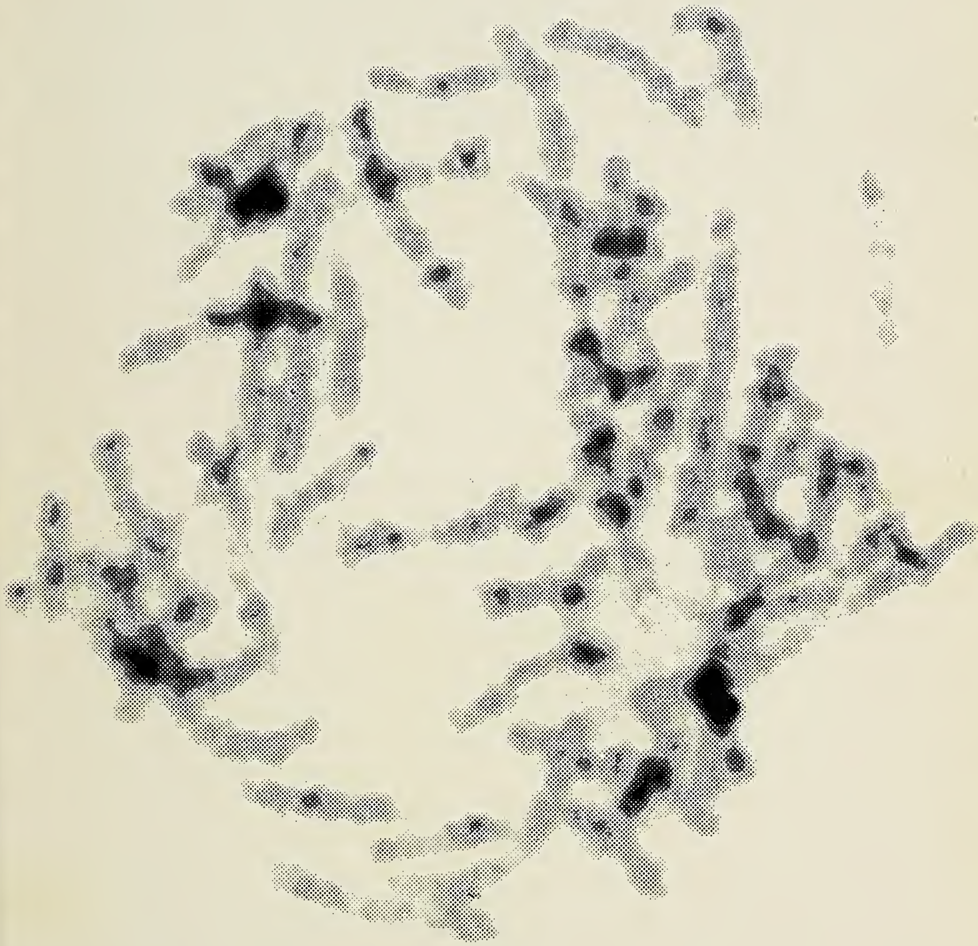

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A Study of *Protesilaus microdamas* (Burmeister) and the Little-known *P. dospassosi* (Rütimeyer) and *P. huanucana* (Varea de Luque) (Papilionidae)

by

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Abstract. Certain wing and genitalic characters of *P. microdamas* are distinctive from other *Protesilaus sens. lat.*. Based on these genitalic distinctions, *P. dospassosi* is associated with *Protesilaus*, and *P. microdamas* in particular, for the first time. *P. huanucana* is accorded species status based on wing and genitalic examination of all *Protesilaus* taxa. Specimens with wings similar to *P. huanucana*, but sharing the distinctive genitalic traits of *P. microdamas* and *P. dospassosi*, are discussed relative to their possibly representing a further terminal taxon of the genus. All of the above taxa have received little or no previous taxonomic examination.

Introduction

Recently, we published taxonomic studies of several groups of Papilionidae (Johnson, Rozycki and Matusik, 1985, 1986a, 1986b; Johnson and Rozycki, 1986). These studies resulted because we were able to assemble samples of several papilionids previously known from only their types or which were apparently undescribed. This research led to cooperation with Dr. Keith S. Brown (Universidade Estadual de Campinas, São Paulo, Brazil) who is preparing a synonymic list of Neotropical Papilionidae, since there was mutual interest in the examination of types and the location of specimens of certain little-known taxa. The present paper summarizes taxonomic results concerning taxa of the genus *Protesilaus* (*sensu* Hancock, 1983). Some results of this study

were published in our paper concerning *P. illuminatus* Niepelt (Johnson, Rozycki and Matusik, 1986b), a taxon previously known from one extant syntype male and accompanying female but of which we were able to assemble recently collected specimens. The results of the present paper concern a cluster of *Protesilaus* taxa which have hitherto been either little-known or of uncertain status.

Study of male genitalia of *Protesilaus* indicated *P. microdamas* (Burmeister) differed from all other *Protesilaus* taxa in lacking the ventral process of the valval harpe. This process is prominent in other taxa of the group. Examination of the unique type of *Papilio dospassosi* Rütimeyer (a taxon inadvertantly misplaced in *Heraclides* by Hancock, 1983, who had not examined the type) indicated that *P. dospassosi* belongs in *Protesilaus* and that its holotype also lacks a ventral valval process. Further study resulted in location of another assemblage of specimens in *Protesilaus* lacking this process. We suspected these represented an undescribed taxon. Since these specimens and *P. dospassosi* were characterized by extreme reduction of red on the hindwing upper surface, and since these and *P. microdamas* lacked the ventral valval process, a previously unrecognized species group within *Protesilaus* was suggested.

Subsequently, Keith Brown discovered that little-known *Papilio huanucana* Varea de Luque (1975) matched the salient appearance of specimens located by us which lacked the ventral valval process. Oddly, however, dissection of representatives of the types series of *P. huanucana* disclosed a much larger valval process than in other *Protesilaus*. Hence, the present study inadvertently discovered several taxonomic characters suggesting species status for *P. huanucana*, but it is doubtful that this species is closely related to *P. microdamas*. The purpose of the following presentation, therefore, will be to review the taxonomic characters of *P. microdamas* and enumerate the several new statuses and synonymies which result from our study of it, *P. dospassosi* and *P. huanucana*. Also, we will discuss the specimens resembling *P. huanucana* which lack the ventral valval process in hope that this review will promote eventual discovery of whether authentic natural populations exist which exhibit the wing markings characterizing *P. huanucana* but lack the ventral valval process characteristic of *P. microdamas* and the holotype of *P. dospassosi*.

Eventual resolution of the precise cladistic relationships in *Protesilaus* will require a full consideration of character polarity in its own and outgroup taxa. Such study cannot be accomplished, however, without definition of the relevant terminal taxa. To this end, the following treatment is provided.

Taxonomic Analysis

Both Munroe (1960) and Hancock (1983) recognized apparent

monophyly in a "*lysithous*-related group" within the genus *Eurytides*. Hancock (1983) accorded this group generic status as *Protesilaus*. According to these authors the group includes the following taxa, which as noted below are tailed or untailed and mimic various other neotropical butterfly taxa: *Short-tailed* or *Untailed* – *pausanius* (Hewitson) [heliconine mimic]; *protodamas* (Godart) [banded, or heliconine mimic depending on form]; *microdamas* (Burmeister); *phaon* (Boisduval) [banded]; chibcha (Fassl); *euryleon* (Hewitson); *hipparchus* (Staudinger); *harmodius* (Doubleday); *trapeza* (Rothschild and Jordan); *xynias* (Hewitson); *ariarathes* (Esper); *ilus* (Fabricius); *branchus* (Doubleday); *belesis* (Bates) [troidine papilionid mimics]. *Long-Tailed* – *thymbraeus* (Boisduval), *lysithous* (Hübner), *kumbachi* (Vogeler), *asius* (Fabricius).

Morphological Structures: Protesilaus, lysithous group, taxa exhibit a single-layered valval harpe (dark, keel-like structure centrad in Figs. 2–6) with a laterally extending spike associated just ventrad and a variously rhomboid structure cephalo-ventrad exhibiting a ventrally extending process. Contrastingly, the sister "*marcellus* group" taxa (*sensu* Munroe, 1961) display a harpe of two parallel layers (as with a keel beneath a keel) without an emphatic associated spike and without a ventrally extending process. The keel-like structure in Figs. 2–6 consists ventrad of two closely paralleled high ridges (drawn in thick solid black) separated by a deep fissure (shown in white or very light gray). The ventrad ridge is variously dentate. The keel can terminate caudad with a variously expressed "head", characteristically single-edged and serrate, double-edged and serrate, or non-serrate in particular species clusters. The laterally pointing spike can be characteristically pointed, furcate, or conical, the ventral process of the rhomboid structure variously emphatic. Characters of the keel of the valval harpe are most useful with those of the laterally pointing spike being less reliable though sometimes distinctive in some taxa.

Phenetic resemblance in the genitalia of short-tailed or non-tailed members of the *lysithous* group of *Protesilaus* generally support the clustering by D'Abrera (1981) based on characters of the wing. Four general groups, disparate from the long-tailed members of the group, are suggested, as shown in the accompanying figures listed below, named in accordance with cluster names proposed by Keith Brown (pers. comm.) and cited with the appropriate D'Abrera (1981) page numbers: the "*phaon* cluster" (pp. 62–63) [Fig. 2], the "*harmodius* cluster" (pp. 64–65) [Fig. 3], the "*ariarathes* cluster" (pp. 66–67) [top]) [Fig. 4], and the "*belesis* cluster": (p. 67 [bottom]) [Fig. 5]. We (Johnson, Rozycki and Matusik, 1986b) have reviewed the major genitalic characters generally defining these clusters.

Major exception to the general morphological similarity in the groups listed above occurs in specimens having no ventral process on the valval harpe. Such include all specimens examined by us or Brown of *P.*

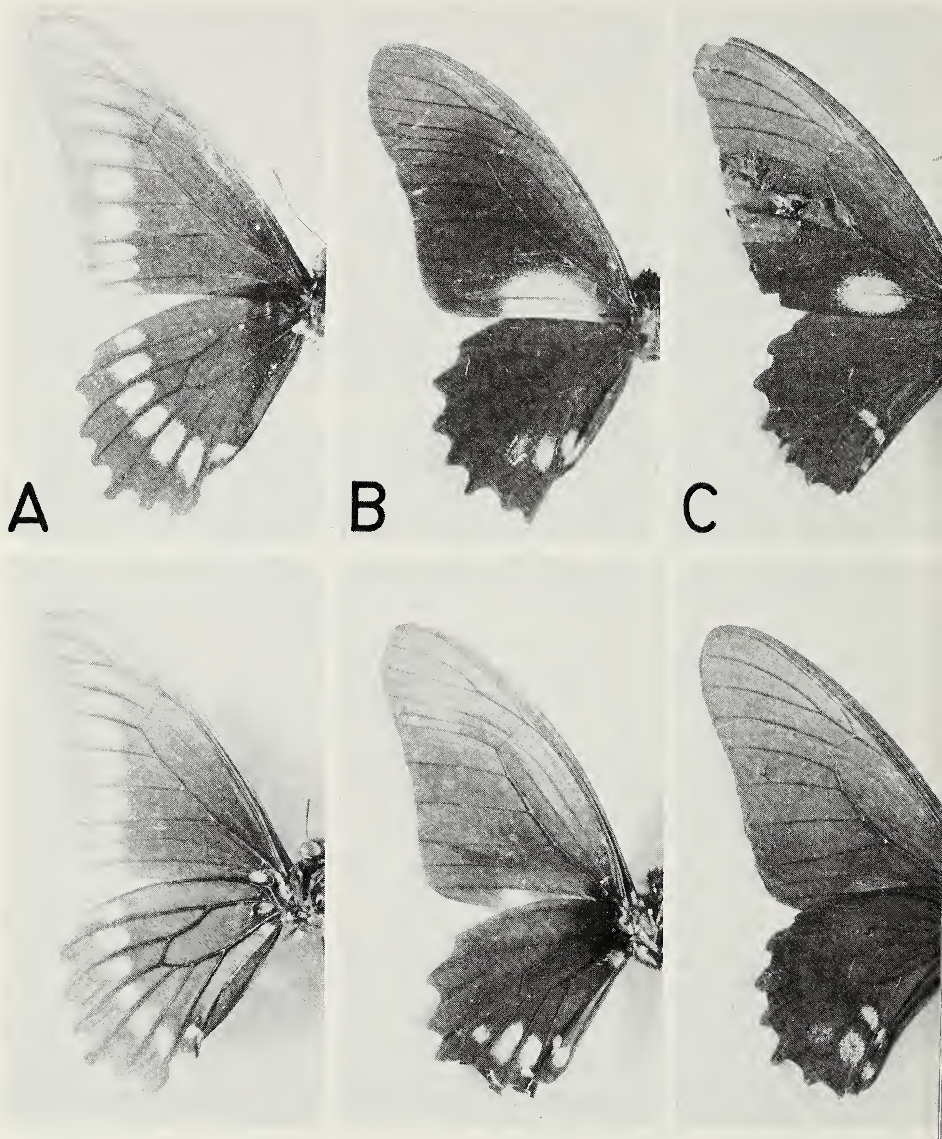


Fig. 1. Upper surfaces (above) and under surfaces (below) of A. *P. microdamas*, male (Sapucay, Paraguay, AMNH); B. *P. huanucana*, male (Tingo Maria, Peru, BMNH); C. *P. dospassosi*, holotype male, (Rio Putumayo, Colombia, AMNH).

microdamas (figured alone by D'Abrera, 1981, p. 63), the *dospassosi* type, and some specimens otherwise like *P. huanucana* [Fig. 6–7]. We thus propose the following species cluster as defined by the following key:

GENITALIC KEY TO MICRODAMAS SPECIES CLUSTER

1. Ventral surface of valval harpe without ventrad-protruding process; and (less reliably) medial process fingerlike structure pointing caudad .... *P. microdamas, dospassosi* and some specimens otherwise like *huanucana* (see treatment later in paper) [Fig. 6]
2. Ventral surface of valval harpe with ventrad-protruding process; and (less reliably) medial process wedgelike, pointing laterally .... all remaining taxa of *Protesilaus* (*sensu* Hancock, 1983) [Figs. 2–5]

Major complication to the identification of *Protesilaus* taxa by wing characters occurs from eastern Ecuador southward through Bolivia because of reduction of upper surface hindwing red in most *lysithous* group taxa of that region. This restriction of red basically to the anal area of the hindwing probably results from a common mimic/model relation involving all the taxa (see Sheppard, Turner, Brown, Benson and Singer, 1984). The following key separates these regionally sympatric *lysithous* group taxa from *P. microdamas* and *P. dospassosi* along with *P. huanucana* and *P. huanucana*-like specimens lacking the ventral valval process. Because these species are usually primarily distinguished by the pattern of red spotting on the upper wing surface, the following key for populations with reduced red relies on characters of the tail and marginal wing spotting. Thus, it will not successfully identify every specimen. However, it will be useful in identifying most.

KEY TO SUPERFICIALLY SIMILAR TAXA

1. Upper surface with both wings banded. .... *P. microdamas* [Fig. 1A]

1A. Upper surface not banded but with a white to yellow mimetic patch caudo-medial on forewing and red spots or orbs in anal and/or anal-medial areas of hindwing 2

2. Upper surface margin of hindwing with yellow dots or slashes in cells, usually from anal margin to cell M_2 and/or M_3 3

2A. Upper surface margin of hindwing without yellow dots or slashes in cells 4

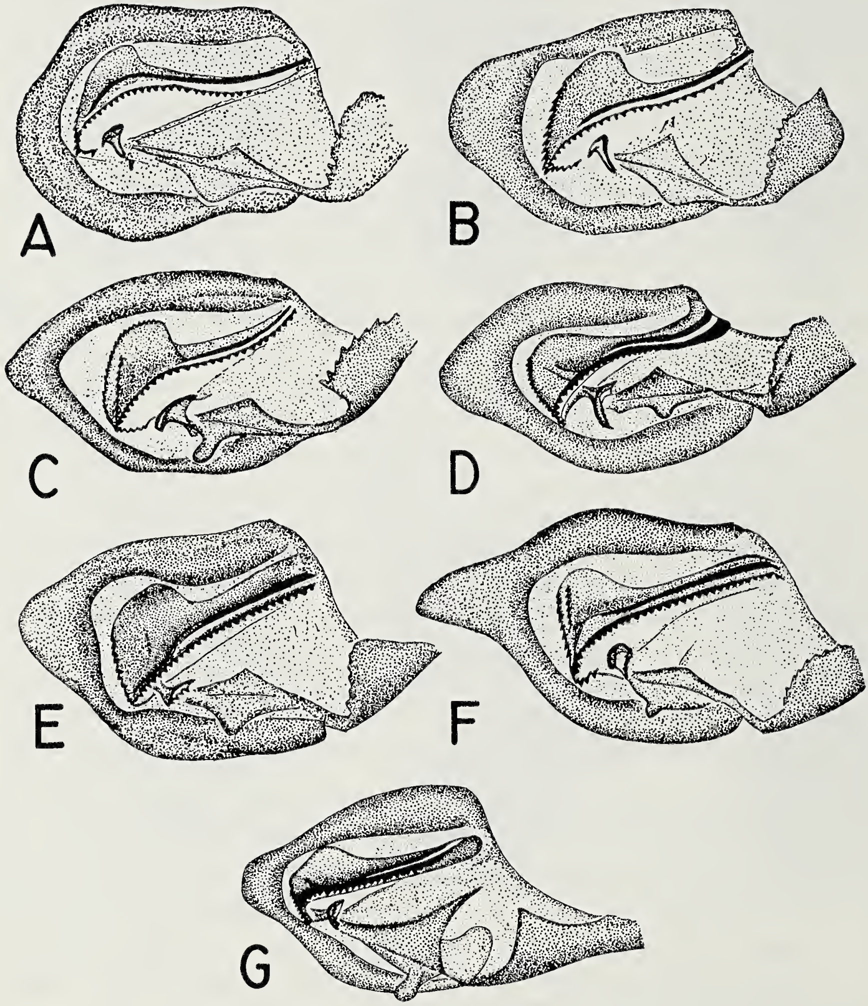
3. Yellow marginal markings are slashes extending costad to cell M_2 and with tail at terminus of cell Cu_1 thinly pointed .... *P. xynias* [Fig. 7A]

3A. Yellow marginal markings are small dots extending costad only

to cell M_3 and with tail at terminus of cell Cu_1 short and stubby .... *P. trapeza* [Fig. 7B]

4. Margin of hindwing with either short stubby tail or thinly pointed tail at terminus of vein Cu_1 5

4A. Margin of hindwing without noticable tail and with vein termini all about equally crennated 6



phaon CLUSTER

Fig. 2. Genitalia of the "*phaon* cluster" (number of dissections, parentheses) A. *pausanias*, Jepelacio, Peru (3); B. *protodamas*, Gavea, Brazil (3); C. *phaon*, Colombia (3); D. *euryleon euryleon*, Costa Rica (3); E. *euryleon haenshi* (Rothschild and Jordan), Balzabamba, Ecuador (3); F. *euryleon pithonius* (Rothschild and Jordan), Cauca Valley, Colombia (3); G. *illuminatus*, Rio Putumayo Valley, Colombia (2).

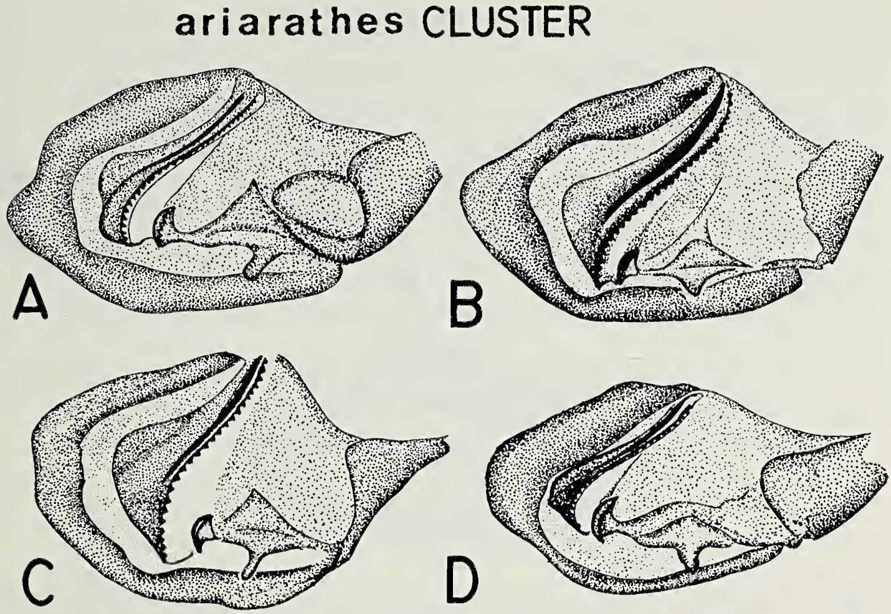


Fig. 3. Genitalia of the "*ariarathes* cluster" (number of dissections, parentheses, other localities, brackets). A. *ariarathes ariarathes,* French Guiana (3); B. *ariarathes gayi* f. *cyamon* (Grey), Middle Rio Ucayali, Peru (3), Alto Jurua, Brazil (1) [additional studied: *gayi gayi*, Janjui, Peru (1), Buena Vista, Bolivia (1); *gayi metagenes* (Rothschild and Jordan), Mt. Duida, Venezuela (1)]; C. *ariarathes menes* (Rothschild and Jordan), Tukeit, Guyana (3). D. *ariarathes*, Janjui, Peru.

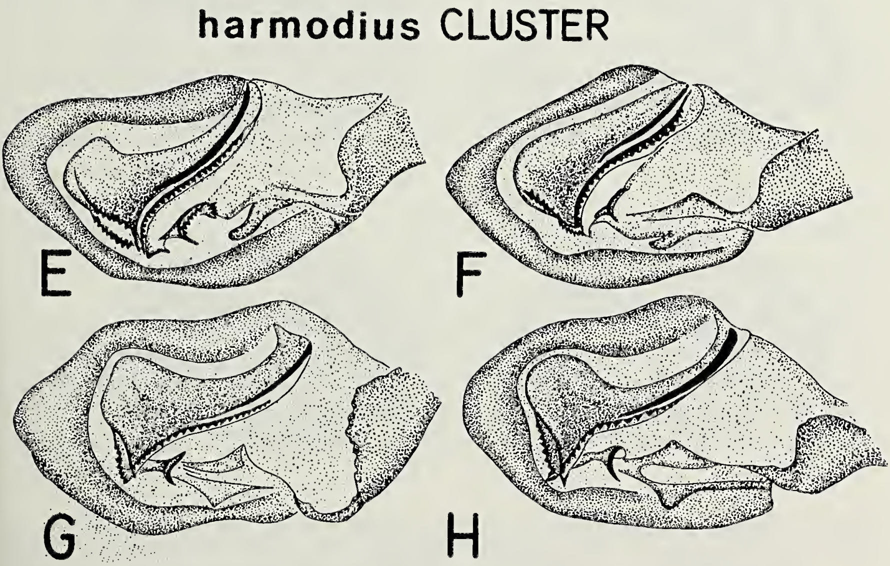


Fig. 4. Genitalia of the "*harmodius* cluster" (number of dissections, parentheses): E. *harmodius harmodius*, Bolivia (3); F. *harmodius xenaides* (Hewitson), Rio Pastaza, Ecuador (3); G. *trapeza*. Rio Napo, Ecuador (3); H. *xynias*, Rio Santiago, Peru (3).

belesis CLUSTER

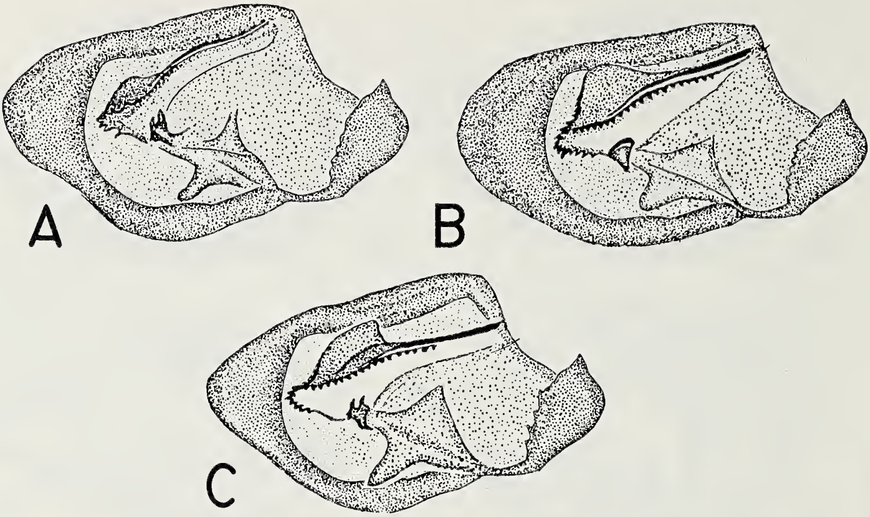


Fig. 5. Genitalia of the "*belesis* cluster": (number of dissections parentheses): A. *belesis*, Soyolapan, Mexico (3); B. *branchus*, San Jeronimo (Chiapas), Mexico (3); C. *illus*, Sosumuco, Colombia (3).

microdamas CLUSTER

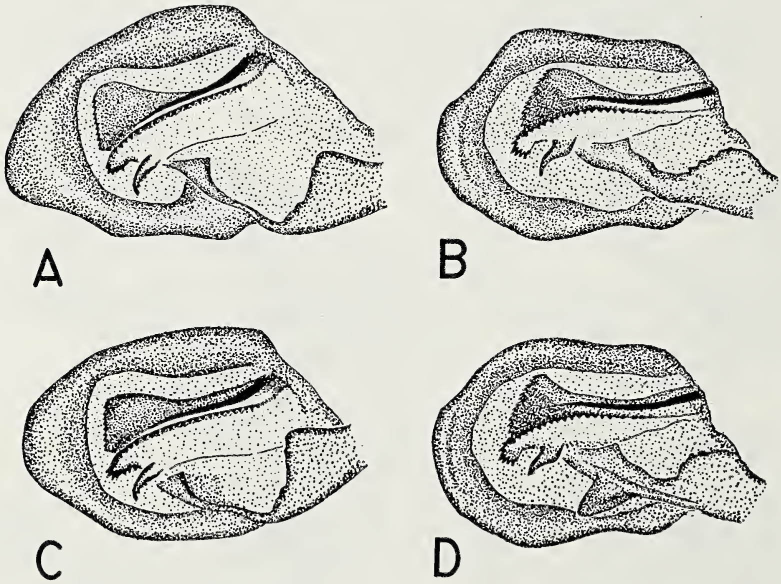


Fig. 6. Genitalia of the "*microdamas* cluster" (number of dissections, parentheses): A. *microdamas*, Sapucay, Paraguay (5, including Santissima Trinidad, Paraguay); B. holotype, *dospassosi*; C. specimen of uncertain status, wings markings like *huanucana* but lacking ventral valval process like taxa of *microdamas* cluster, Rio Santiago, Peru (4) including specimens listed in Fig. 7; D. *P. huanucana*, from Ehrmann series (CMNH), Sarajacu, Ecuador.

5. Red markings in anal areas of cells CU_1 and CU_2 7
5A. Red marking in anal areas reduced or obsolescent so as pattern in CU_1 and CU_2 not discernable 8
6. Ventral surface of valval harpe with large ventrad protruding process . . . . *P. huanucana* [Fig. 1B]
6A. Ventral surface of valval harpe without ventral process . . . . specimens of uncertain identity referenced in text.
7. Hindwing with upper surface red spots in anal area cells CU_1 and CU_2: two median (CU_1, CU_2), one postmedian (CU_1); dorsal surface of keel of valval harpe moderately wide cephalad . . . . *P. dospassosi* [Fig. 1C]
7A. Hindwing with upper surface red spots in anal area cells CU_1, CU_2 and 2A: two median (CU_2, 2A), one postmedian (CU_2); dorsal surface of keel of valval harpe extremely wide cephalad 8
8. Ground color blackish, margin of hindwing with either short stubby tail (*a. gayi*) or thinly pointed tail (*a. ariarathes*) at terminus of vein CU_1 . . . . *P. ariarathes* [Fig. 7C]
8A. Ground color brown to lighter brown without noticable tail and with vein termini of hindwing all about equally crenated 6

Annotated Taxonomic List (Including New Synonymies and Statuses)

***P. microdamas* species cluster:**

Protesilaus microdamas (Burmeister), Figs. 1A, 6A

Papilio microdamas Burmeister 1878. Description Physique de la Republique Argentine. Lepidopteres 5: 63.

Adult. Fig. 1A. Length of forewing: $\bar{X}$ of 5 males (AMNH), 40.2 mm., range 39.0 to 42.0 mm. Male Genitalia: Fig. 6A. Location of type: unknown. Type Locality: Corrientes, Argentina. Distribution: From sparse representation in collections, ascertained as at least Paraguay, Matto Grosso State, Brazil and most probably some adjacent areas.

Remarks. A banded species, *P. microdamas* is not confusable with any congener. However, its taxonomic affinity has been unclear and it is extremely rare in collections. A series of 25 males and females at the AMNH (of which only 5 are males) from Santissima-Trinidad, Cordillera Province, Paraguay, collected by B. Podtiaguin from May to August in an unnoted year, is the largest series in North American institutions. Other North American museums and British Museum (see Acknowledgments) together have fewer than 15 specimens. The rarity of females of *Protesilaus* taxa suggests the large Podtiaguin sample probably represents an unusually fortuitous collecting locality for the species.

Protesilaus dospassosi (Rütimeyer), new combination, Figs. 1C, 6B

Papilio dospassosi Rütimeyer 1969. J. Lepid. Soc. 23: 255–257.

Adult. Fig. 1C. Length of forewing: holotype, male, 37.5 mm. Male Genitalia: Fig. 6B. Location of type: AMNH. Type locality: Rio Putumayo, Colombia. Distribution: Known only from type locality.

Remarks. As noted previously, Hancock (1983) inadvertantly misplaced this taxon in the genus *Heraclides* (tribe Papilionini) since he had not examined the type. Keith Brown (pers. comm.) suggested the need to differentiate *P. dospassosi* from *P. morrisi* Ehrmann (Ehrmann, 1921; Holland, 1927) a taxon somewhat similar in original description. We have examined the type of *P. morrisi* at the CMNH, a male from "Loja, SE Ecuador, 30 November 1914, Rev. Hyde Collection". The type and a group of associated specimens identified by Ehrmann all have postmedian red spots costad to cells 2A and CU_2, and by genitalic dissection are clearly allied to *P. harmodius*, of which *morrisi* should probably be considered a subspecies. Keith Brown informs us that he has seen a possible specimen of *P. dospassosi* in the collection of the Los Angeles County Museum.

The apparent species status and insular distribution of *P. dospassosi* should be considered in light of its local sympatry with several other extremely insular butterfly taxa equally rare in collections surveyed by us. These include: *P. illuminatus* (Niepelt) (Johnson, Rozycki and Matusik, 1986b), known from only nine specimens; the nymphalid butterfly *Anaeomorpha splendida* Rothschild (only four specimens located by Johnson and H. Descimon [Universitie de Provence, Marseilles, France] at AMNH, BMNH or Muséum National d'Histoire Naturelle (Paris) and of which species a subspecies *columbiana* Niepelt (1928) was named, and is known only from, two specimens taken near the type locality of *P. dospassosi*; and an apparently undescribed subspecies of *Prepona werneri* Hering and Hopp known from a single specimen obtained by Johnson and Matusik from the same collectors capturing *P. illuminatus* in 1981. According to a museum survey by Johnson and Descimon, *P. werneri* is itself known from fewer than 10 specimens, though the exact number is uncertain since most are owned by private collectors.

It remains to be clarified whether further specimens of *P. dospassosi* will corroborate or falsify the notion that lack of the ventral valval process, as in the holotype, indicates sister species relationship with *P. microdamas*.

Other Taxa:

Protesilaus huanucana (Varea de Luque), new combination, revised status Figs. 1B, 6D

Graphium trapeza huanucana Varea de Luque, 1975. Shilap. Rvta. Lep. 3(9): 28–32.

Adult. Fig. 1B. Length of Forewing: $\bar{X}$ of 5 specimens in Ehrmann series (CMNH), 39.8 mm., range 38.0 – 42.0 mm. Male Genitalia: Fig. 6D. Location of type: British Museum (Natural History). Type Locality: Tingo Maria, Peru. Distribution: noted from dissected specimens by Keith Brown (pers. comm.) as including southwest Colombia, eastern Peru, Acre, Rondonia and Amazonas states, Brazil and northern Bolivia.

Remarks. Hitherto, Varea de Luque's publication of the name *huanucana* has received no further report in the literature. The taxon is distinctive, a fact which formerly led us and Brown (at AMNH, 1972) to note it as undescribed or not identifiable. Also, Varea de Luque suggested that *huanucana* might be "quiza *bona species*." It is distinguishable from congeners by the extreme reduction of red spotting on the upper surface of the hindwing (limited to anal

area only) and by its cream-yellow mimetic patch on the forewing upper surface. Amongst other taxa with regionally reduced upper surface red, it is distinguishable by other characters (see Key). These characters, along with those of the genitalia have led us and Brown to consider it as a valid species pending biological studies. The existence of this taxon was also recognized by Ehrmann who designated a type (CMNH) for a manuscript name which was never validly published (Holland, 1927). Ehrmann's study series was from "Sarayoi'u, E. Ecuador" or "Sarajacu, Oriente, Ecuador" undated and from E. T. Owen in the Buckley Collection. Our dissection of these specimens shows that all examined have a ventral valval process and are thus *P. huanucana*.

Process-less Specimens Otherwise like *P. huanucana*:

Adult. Fig. 7D. Length of Forewing: $\bar{X}$ of 3 males, AMNH, 41.8 mm., range 41.0 to 42.5 mm. Male Genitalia: Fig. 6C. Distribution: from dissections by the authors: AMNH – Rio Santiago, Peru; Rio Purus, Brazil; Costa Rica, Bolivia; David Matusik Collection – Costa Rica, Bolivia.

Remarks. Among specimens generally resembling *P. huanucana* a number of specimens have been found which lack the ventral valval process and are thus like *P. microdamas* and *P. dospassosi* (Fig. 6). A high frequency of these was found when we first began sorting from collections *P. huanucana*-like specimens which we suspected represented an undescribed entity. When Brown discovered the apparent external similarity between our series and the *P. huanucana* types he further discovered these latter had a large ventral valval process. Subsequently, by looking at a larger range of specimens, we also found such examples. A number of lepidopterists have been consulted concerning this and there is concensus that the smoothly edged cephalo-ventral surface of the valval harpe on which a ventrad pointing process has not developed must be considered as a possibly strong character within *Protesilaus*. Also, we and John Rawlins (CMNH) agree there are some differences in the wing markings of the specimens without the ventral valval process which suggest they are often separable from *P. huanucana*. The former appear more brown (as opposed to black or blackish) than *P. huanucana* and evidence a more evenly crennated hindwing margin and a more yellow to ochre forewing mimetic patch.

It is important to ascertain whether specimens lacking the ventral valval process represent simple and insignificant variation aside from the consistency of the valval process character in *P. microdamas*, are individuals representing reversion to a primitive process-less configuration characteristic of plesiomorphy in *Protesilaus*, or whether authentic natural populations occur with the *P. microdamas*-like valval harpe being taxonomically significant. If the latter is true, such populations would constitute another important terminal taxon in the cladistic structure of the genus.

Summary and Conclusions

Study of wing and male genital characters in the genus *Protesilaus* indicates *P. microdamas* differs significantly from congeners and that at least one other taxon, *P. dospassosi* (hitherto not placed in *Protesilaus*), shares with *P. microdamas* a valval harpe with a smoothly edged ventral surface. Other *Protesilaus* specimens have been found with a

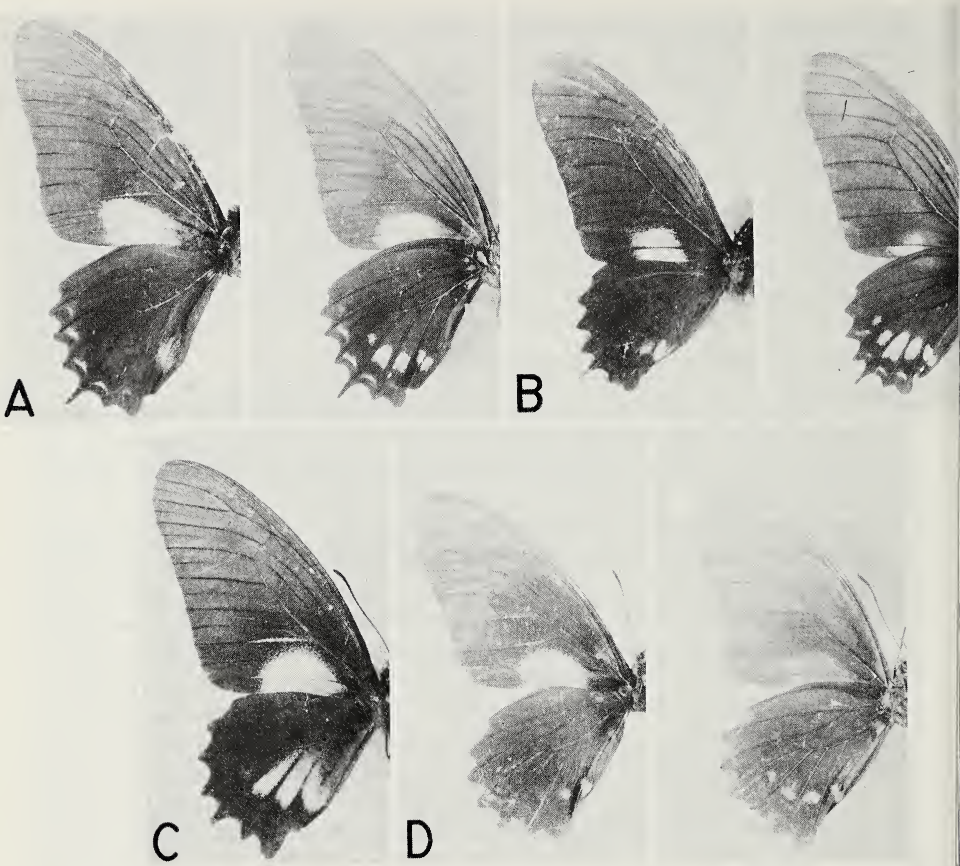


Fig. 7. Examples of wing patterns from "Key to Superficially Similar Taxa" and specimens resembling *P. huanucana* but lacking ventral process on valval harpe. A. *P. xynias*, male (left, upper surface; right, under surface) Rio Santiago, Peru, AMNH; B. *P. trapeza*, male (left, upper surface; right, under surface) Rio Napo, Ecuador, AMNH; C. *P. ariarathes*, male (upper surface; extent of under surface marking similar) Janjui, Peru, AMNH; D. example of specimens somewhat resembling *P. huanucana* but lacking ventral process on valval harpe. These may represent an undescribed taxon, male (left, upper surface; right, under surface) Costa Rica, Bolivia, AMNH.

similar, processless, ventral harpe surface. Still others, similar in wing facies to these latter have a large ventral process and comprise the taxon *P. huanucana*. This taxon, distinctive in a number of characters from other *Protesilaus*, is suggested as a species level taxon whose biology should be studied in detail. The status of specimens like *P. huanucana* lacking the ventral valval process is unresolved. If authentic natural populations are found which evidence this latter character, such populations must be suspected as representing a further terminal taxon for the genus.

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Hand-pairing of *Papilio glaucus glaucus* and *Papilio pilumnus* (Papilionidae) and hybrid survival on various food plants

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Abstract. Hand-pairing of a female *Papilio glaucus* with a male *P. pilumnus* resulted in the hatching of 69 larvae. Hybrid larvae survived on species of Lauraceae, and also on species of Rutaceae and Magnoliaceae. Hybrid larvae did not initiate feeding on black cherry. Both larvae and the adult males that were produced were intermediate between the two species in a variety of morphological traits.

Introduction

The three-tailed swallowtail, *Papilio pilumnus* Boisduval occurs from southern Arizona and Texas southward to Guatemala (Beutelspacher and Howe, 1984). Howe (1975) observed oviposition on a species of *Litsea* (Lauraceae) in Chiapas, Mexico, however relatively little is known about its larval stages or field biology (but see Scott, 1986). Because of its superficial resemblance to adult tiger swallowtails (Fig. 1). *P. pilumnus* generally had been considered to be a member of the *Papilio glaucus* L. species group until Brower (1959) placed it with the *Papilio troilus* L. group. Three factors support the placement of *P. pilumnus* with the *P. troilus* group. The male genitalia are more like those of *P. troilus* (Brower, 1959). As originally described by Schaus (1884), *P. pilumnus* larvae more closely resemble *P. troilus* and *P. palamedes* than any of the *P. glaucus* group species. In addition, pupal color and morphology (Schaus, 1884) are more like *P. troilus* and *P. palamedes*. Tyler (1975), however, suggested that *P. pilumnus* is transitional between the *P. glaucus* and *P. troilus* species groups.

In our ongoing studies of the physiological and biochemical mechanisms of differential foodplant use in North American *Papilio glaucus* and *Papilio troilus* species and subspecies, we have hand-paired various taxa in more than 4000 crosses (see Scriber, 1987a,b,c). Among the most interesting were our pairings of virgin *Papilio glaucus* females with field captured *P. pilumnus* males. In this paper, we describe the hybrid offspring of these pairings and their abilities to use potential foodplants.

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Methods:

To obtain virgin females, we first collected adult females of *Papilio glaucus*, *P. troilus*, and *P. alexiares* from the field. Females were allowed to oviposit individually on acceptable foodplant leaves (black cherry and sassafras) kept fresh by water-filled aquapics®. Females were housed in clear plastic boxes (12cm x 20cm x 30cm) heated by a 100w incandescent lightbulb placed approximately 0.5m from the boxes. Eggs were removed on leaves at 2 day intervals after oviposition and neonate larvae were subsequently reared on excised leaves of various species of plants (in 4cm x 15cm petri dishes with screened ventilation) to pupation. Larvae were reared in controlled environment growth chambers (at 16:8 photo/scotophase with a corresponding temperature regime of 23.5/19.5 degrees C). Foodplant leaves were kept turgid by use of water-filled aquapics (Scriber, 1977), and changed as needed. A mixture of healthy-looking mature (fully-expanded) leaves and younger leaves were used for neonate studies. After weighing, pupae were individually placed in 14 cm screen cages until adult emergence.

Hand-pairings of virgin female butterflies to field-collected males were conducted as in Clarke & Sheppard (1956) with the pair hanging in a screen cylinder (approximately 12cm tall by 14cm diameter) covered by the top and bottom of a petri dish. Females that had been in copulation at least 30 minutes were set up in the oviposition boxes as described above. Newly eclosed larvae were individually transferred with a camel hair brush and distributed among the various foodplants. After females died, they were dissected and examined for spermatophores.

Results:

Males and females of *Papilio pilumnus* were collected by M. Evans, D. Robacker, and W. Warfield in the states of Nuevo Leon and Tamaulipas in northeastern Mexico and brought to the laboratory. One *P. pilumnus* female produced 2 eggs, but no larvae. A second *P. pilumnus* female laid 5 eggs. The single larva did not survive on red bay. A third *P. pilumnus* female laid 4 eggs; the single hatchling developed on sassafras. Although a total of five hand-pairings lasted 30 minutes or longer, in three, no spermatophore was passed (one with *P. troilus*, #4245, one with *P. alexiares*, #3301, and one with *P. glaucus*, #4235). Only one pairing with a *P. glaucus* (#4231) produced fertile eggs. Of a total of 108 eggs, 69 larvae eclosed, 7 died while crawling out of their eggs, 7 additional eggs appeared to be fertile but produced no larvae, and 25 eggs appeared to be infertile.

No neonate hybrid larvae survived on black cherry, paper birch, quaking aspen, or sycamore (Rosaceae, Betulaceae, Salicaceae, and Platanaceae, respectively; see Table 1). There was no indication that the larvae initiated feeding on these hosts. However, species from the Rutaceae (hop tree), Magnoliaceae (sweet bay and tulip tree), and Lauraceae (spicebush, red bay, and sassafras) were accepted by the neonate larvae and nearly 50% survived to the second instar (Table 1). Larvae surviving to the second instar on plants other than sassafras and

Table 1. Neonate larval survival of F_1 hybrid larvae of the cross (*Papilio glaucus* female) x (*P. pilumnus* male).

Plant Species	Plant Family	Surviving(n) to second instar	Total set up	% Survival
Prunus serotina Ehrh. (Black Cherry)	(Rosaceae)	0	27	0
Betula papyrifera Marsh. (Paper Brich)	(Betulaceae)	0	6	0
Populus tremuloides Michx. (Quaking Aspen)	(Salicaceae)	0	3	0
Platanus occidentalis L. (Sycamore)	(Platanaceae)	0	3	0
Ptelea trifoliata L. (Hop Tree)	(Rutaceae)	1	2	50
Magnolia virginiana L. (Sweetbay)	(Magnoliaceae)	1	4	25
Liriodendron tulipifera L. (Tulip Tree)	(Magnaliaceae)	4	8	50
Lindera benzoin (L.) Blume (Spicebush)	(Lauraceae)	1	4	25
Persea borbonia (L.) Spreng. (Red Bay)	(Lauraceae)	2	6	33
Sassafras albidum (Nutt.) Nees (Sassafras)	(Lauraceae)	5	6	83

tulip tree were switched to one of these species for rearing. Of the 14 larvae surviving the feeding trials, 5 successfully pupated (Table 2). All resulting adults were male. No attempt to determine the fertility of these males was made.

The adult male hybrids are intermediate in wing pattern and shape between the *P. glaucus glaucus* males and *P. pilumnus* males on both the dorsal (Fig. 1a, b, c) and ventral (Fig. 2a, b, c) sides. It is also clear that the final larval instar reflects a composite of traits from each species. Unlike *Papilio glaucus* which is a solid green color (Fig. 3a), the hybrid larva (Fig. 3b) has a yellow line running along the side of the body with a brown ventral color and a series of blue spots on the abdominal segments just below this line as desribed for *P. pilumnus* (Fig. 3c) (Schaus, 1884; Brower, 1959), *P. palamedes* (Fig. 3d), and *P.*

Table 2. A summary of data for five *P. glaucus* x *P. pilumnus* larvae which pupated.

Larval Hatch Data (Aug 1986)	Larval Food	Pupation Date (Sept.)	Larval Duration (days)	Pupal wt. (gm.)	Adult Emergence Date (1986) (All Males)	Pupal Duration (days)
18	Redbay-Tulip Tree	20	33	no. wt.	1 Oct.	11
18	Tulip Tree	10	23	0.3229	Dead as a pharate adult by late Oct	—
19	Spicebush-Sassafras	26	38	0.4692	7 Oct Deformed Adult	11
19	Sassafras	12	24	0.5089	23 Sept. Deformed Adult	11
19	Sassafras	12	24	0.5174	23 Sept. Deformed Adult	11

troilus (Fig. 3e). Unlike *P. palamedes*, *P. troilus*, and *P. pilumnus*, the hybrid larva has a false thoracic eyespot without a solid black center (Fig. 3b, 3c, 3d, 3e) which closely resembles the false eyespot of *P. glaucus* (Fig. 3a). The brown larval stage (before pupation) of the hybrid larva (Fig. 4) lacks the transverse yellow at the base of the thorax which characterizes *P. glaucus* (Fig. 3a). the hybrid pupae were small (presumably due to nutritional factors) and were more *troilus*-like than *glaucus*-like in general shape (Fig. 5). As described for *P. pilumnus* pupae (Brower, 1959), these hybrid pupae were pinkish in color and laterally ridged, which is unlike those of all *P. glaucus* group species.

Discussion:

The survival and developmental compatibility in these *P. glaucus/P. pilumnus* hybrid genomes were surprising, especially when compared with other interspecific pairings we have conducted between various *P. glaucus* and *P. troilus* species group members. Viability of the *glaucus/pilumnus* hybrids was comparable with that of interspecific hybrids

within the *glaucus* group but greater than that of previous *glaucus* group/*troilus* group hybrids. For example, the average viability (larvae/eggs) of the two *glaucus/pilumnus* pairings here was 35.2% (70.4, 0), compared to pairings of *P. glaucus* females with males of *P. multicaudatus* (n=10; x=44.0%) *P. eurymedon* (n=18; x=30.2%), *P. rutulus* (n=8; x=31.1%), and *P. alexiares* (n=15; x=56.1%). Although attempted numerous times only one successful pairing of a *P. glaucus* female with a *P. troilus* male has ever been obtained (i.e. copulation for more than 30 minutes), and none of the eggs produced hatched. We have achieved 3 successful hand-pairings of *P. palamedes* males with female *P. glaucus*. One such pairing produced viable offspring. It should be pointed out, however, that a number of factors other than genetic compatibility are likely to be involved in determining egg viability, and considerable caution in the interpretation of fertility data is advised (eg. see Lederhouse and Scriber, 1987).

The ability of these hybrid larvae to eat, survive, and grow on the Lauraceae was not surprising since this is the only family the related *P. troilus* and *P. palamedes* may actually utilize (Scriber, 1986), and *Papilio glaucus* can utilize lauraceous species to a certain extent (with the exception of red bay) (Scriber, et al. 1975; Scriber, 1973, 1984, 1986, 1987c). The ability of hybrid larvae to use Rutaceae and Magnoliaceae may reflect the contribution of *P. g. glaucus* to their genome or latent ancestral capabilities. Although it generally has been presumed that the Lauraceae were ancestral foodplants with a key role in the evolution of *Papilio* (Forbes 1932, 1958; Munroe, 1948, 1960), the Rutaceae (Munroe and Ehrlich, 1960; Scriber, 1972; Hancock, 1983;) and the Magnoliaceae (Dethier, 1941, Ehrlich and Raven, 1965) could be equally important. Feeny, et. al. (1983) summarized the potential chemical common denominators among these plant families.

Perhaps the most interesting aspect of these hybrid *glaucus/pilumnus* foodplant bioassays were the plants that larvae did not successfully use (Table 1). In particular, black cherry (*Prunus serotina*) and paper birch (*Betula papyrifera*) are two of the plant species that all members of the *Papilio glaucus* species group readily consume (including *P. rutulus*, *P. eurymedon*, *P. glaucus glaucus*, *P. g. canadensis* and *P. alexiares*; Scriber, 1987b, 1987c). The hybrid larvae did not initiate feeding on either black cherry or paper birch apparently not recognizing them as potential hosts. Unlike the hybrid transfer of detoxication abilities between Salicaceae feeders (*P. rutulus*, *P. eurymedon* and *P. g. canadensis*) and Magnoliaceae feeders (*P. g. glaucus*, *P. g. australis*, *P. alexiares*; Scriber, 1987a), it remains unclear if the *P. glaucus* abilities to use Betulaceae and Rosaceae were transferred to the hybrid larvae (*glaucus* x *pilumnus*) in this study. Sample sizes are low, and additional crosses seem warranted because there is an interesting genetic story regarding detoxication (and perhaps phylogenetic history) to be worked out here.

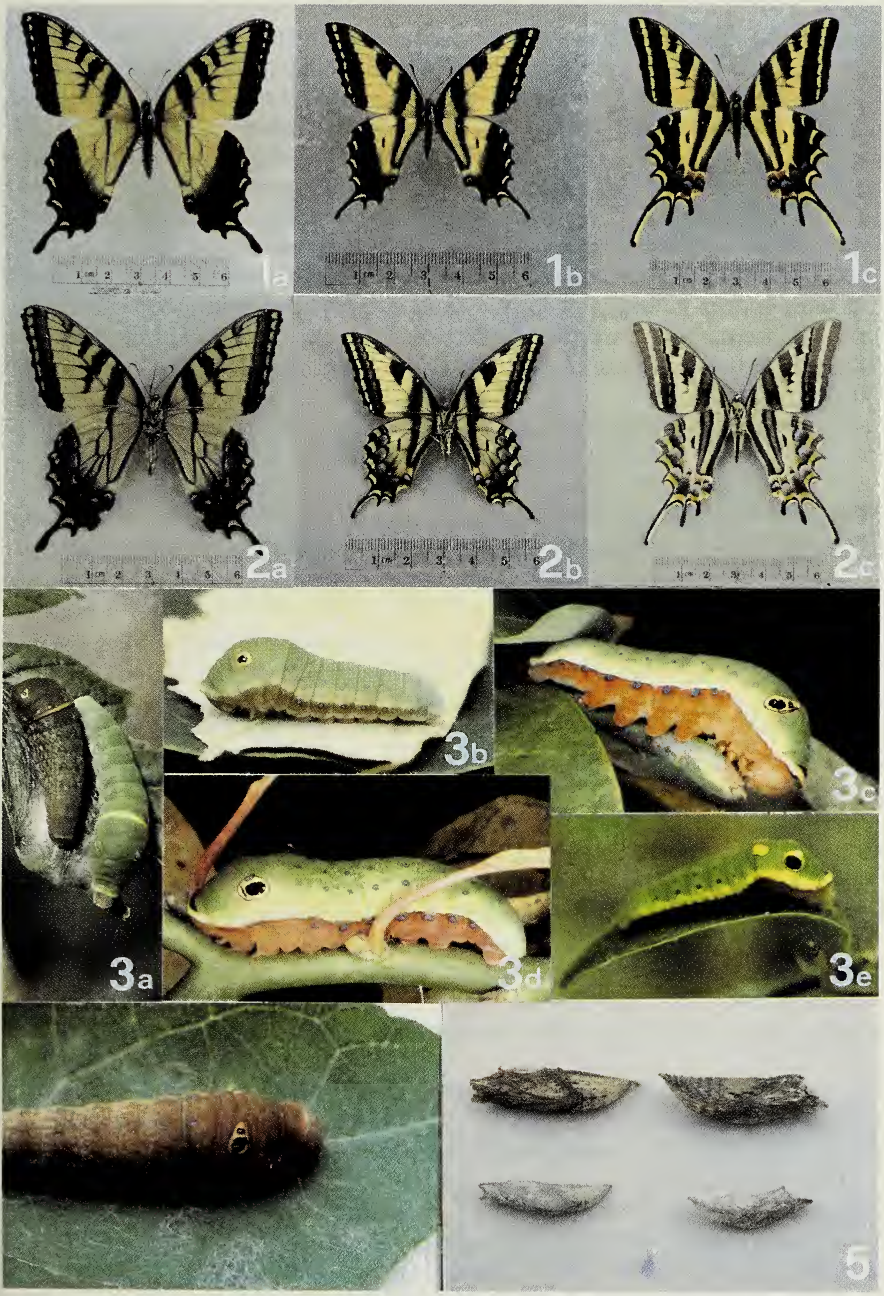

Fig. 1. Dorsal view of adult males of: a) *P. g. glaucus* b) hybrid *P. g. glaucus* (female) x *P. pilumnus* (male) c) *P. pilumnus*

Fig. 2. Ventral view of specimens in Fig. 1

Fig. 3. Final (5th) instar of: a) *P. g. glaucus*, brown and green morphs. b) hybrid *P. g. glaucus* x *P. pilumnus* c) *P. pilumnus* d) *P. palamedes* e) *P. troilus*

Fig. 4. Hybrid larva (*P. g. glaucus* x *P. pilumnus*) that has turned brown prior to pupation

Fig. 5. Ventral and lateral view of the hybrid pupae (bottom) contrasted to the same views of *P. glaucus* pupae (top)

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New Host Records and Morphological Notes on Four Tortricines (Tortricidae)

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Hypericum perforatum (Guttiferae), St. John's-wort or Klamath weed, a plant of European origin, has been introduced into many regions of the world, including rangelands of the United States, Canada, South Africa, and Australia (Harris and Peschkin, 1974; Giese, 1980). St. John's-wort is considered a rangeland weed because it produces the phototoxic compound hypericin, a blister-inducing agent for livestock in the presence of sunlight (Blum, 1941). Because there are few published records of Lepidoptera feeding on *Hypericum* in North America (Kingsolver et al., 1984), we now report on four native North American tortricids reared from two species of *Hypericum*.

Larvae of *Platynota flavedana* Clemens, *Choristoneura parallela* (Robinson), *Sparganothis sulfureana* (Clemens), and *Xenotemna pallorana* (Robinson) were found in leaf ties on *H. perforatum* at several Illinois localities; the latter two species were also found at one site in Michigan. In addition, the last three species were collected in Illinois from *H. sphaerocarpum*, a native North American species that does not contain hypericin. For each tortricid species, as is applicable, *H. perforatum* and *H. sphaerocarpum* represent new host records (MacKay, 1962; Chapman and Lienk, 1971), although *S. sulfureana* has been reared from an undetermined species of *Hypericum* (Godfrey et al., in press). All four species are polyphagous feeders (see Table 1) with the majority of previous host records on agricultural crops (Chapman and Lienk, 1971). Identification of field-collected larvae was based on individuals reared to adult. For each species of tortricid, the hosts and collection data are provided, accompanied by morphological notes on the immature stages to supplement the existing keys in Chapman and Lienk (1971), MacKay (1962), and Mosher (1916).

Platynota flavedana is a pest on strawberry (Wilde and Semel, 1966). Larvae of *P. flavedana* were collected on *H. perforatum* from the end of June through August 1985 along roadsides of several Illinois localities: near Monticello (Piatt Co.), Mount Vernon (Jefferson Co.), Carbondale (Jackson Co.), and Marion (Williamson Co.). *P. flavedana* was common on *Hypericum* in 1985 but was not found in 1986.

Sparganothis sulfureana is recorded from a wide variety of plants,

Table 1. Host records of 4 species of Tortricidae larvae collected and reared on *Hypericum perforatum.*

SPECIES	HOST RECORDS
Choristoneura parallela	Compositae, Ericaceae, Guttiferae*, Leguminosae, Myricaceae, Rosaceae, Rubiaceae, Rutaceae
Platynota flavedana	Aceraceae, Begoniaceae, Compositae, Ericaceae, Guttiferae*, Leguminosae, Malvaceae, Rosaceae
Sparganothis sulfureana	Ericaceae, Gramineae, Guttiferae*, Leguminosae, Pinaceae, Ranunculaceae, Rosaceae, Salicaceae, Umbelliferae, Verbenaceae
Xenotemna pallorana	Caryophyllaceae, Compositae, Guttiferae*, Leguminosae, Pinaceae, Rosaceae, Verbenaceae

* Represents a new host record
References: Beckwith, 1938; Chapman and Leinke, 1971; Deitz et al., 1976; Freeman, 1958; MacKay, 1962; Martin, 1958; Newcomer and Carlsen 1952; Wilde and Semel, 1966.

including many cultivated species. Considered a pest on cranberry, *S. sulfureana* is commonly known as false yellowhead or sulfur leafroller (Beckwith, 1938; Chapman and Lienk 1971). Larvae of *S. sulfureana* were commonly collected on *H. perforatum* from late June through August 1985 and 1986, at the same Illinois locations previously mentioned for *P. flavedana.* In addition, larvae of *S. sulfureana* were also collected from *H. perforatum* at the University of Michigan Biological Station (near Pellston, Michigan) in July 1985 and from *H. sphaerocarpum* near Monticello and near Forrest, Illinois (Livingston Co.) in July 1985 and 1986.

Xenotemna pallorana is a minor pest on young pines (Martin, 1958), young apple and other fruit trees (Newcomer and Carlson, 1952). While common, larvae were found only in July of 1985 and 1986 feeding on *H. perforatum* at the same Illinois localities previously mentioned and at the University of Michigan Biological Station. Larvae were also collected from *H. sphaerocarpum* near Monticello, Illinois in July 1986.

Choristoneura parallela also has a wide host range. Commonly known as the spotted fireworm, *C. parallela* is considered a pest on cranberries. The larvae were collected on both species of *Hypericum* near Monticello,

Illinois during July, 1986. They were found frequently on *H. sphaerocarpum* but only once on *H. perforatum* at this site. Larvae were also collected in July at a site east of Urbana, Illinois (Champaign Co.) on *H. sphaerocarpum*.

Although the caterpillars of *X. pallorana* and *C. parallela* are relatively easy to recognize compared to other *Hypericum*-feeding tortricids (see MacKay 1962 for descriptions), larvae of *P. flavedana* and *S. sulfureana* can easily be confused in the field. Chapman and Lienk (1971) illustrated the larva of *S. sulfureana* in color and distinguished it from *P. flavedana* by the presence of a thin black line along the lateral margins of the prothoracic shield. However, some *P. flavedana* may also have this black line. A more consistent field character involves the thoracic and abdominal pinacula of the dorsal setae. Most dorsal pinacula in *Platynota* spp. are elongated lengthwise whereas in *S. sulfureana* all the pinacula are round (Chapman and Lienk 1971; MacKay, 1962). In addition, Chapman and Lienk (1971) correctly noted that *S. sulfureana* may be separated from *P. flavedana* by the dark dorsum contrasting with the paler ventral region. In *P. flavedana* the dorsal area is concolorous with the rest of the body. MacKay (1962) distinguished *P. flavedana* from other *Platynota* spp. by its clear brownish-yellow head, prothoracic shield, and prothoracic pinacula. However, this distinctive coloration is only found on the last two instars. Younger larva have a black prothoracic shield and head (Wilde and Semel, 1966) and thus, cannot be identified using the above characters.

Mosher (1916) separated the pupa of *P. flavedana* from *S. sulfureana* by the presence of flattened cremaster setae and the absence of a row of spines on the second abdominal segment in the female. Some more obvious morphological differences between these species (that may prove to be a useful tool in the systematics of tortricines in general) involves variation in the shape of the vertex and the presence of maxillary palpi. *Platynota flavedana* has maxillary palpi and a round vertex which lacks a ridge (Fig. 1). In contrast, the pupa of *S. sulfureana*

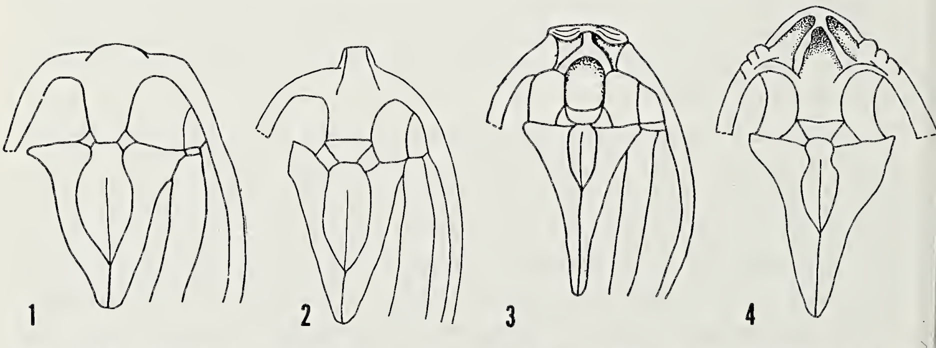

Fig. 1-4. Ventral view of four tortricine pupae (30x). 1. *P. flavedana* 2. *S. sulfureana*; 3. *C. parallela*; 4. *X. pallorana*.

lacks maxillary palpi and has a ridge which extends cephalad from the frons to the epicranial suture (Fig. 2). A similar ridge is found in *C. parallela* (and other *Choristoneura* spp.) but it runs between the antennal scapes (Fig. 3). *X. pallorana* was not included in Mosher's (1916) key but the characteristic vertex (Fig. 4) readily distinguishes this species from other *Hypericum*-feeding tortricids in Illinois.

It is of interest that four native generalist tortricid species have been found commonly feeding on an introduced plant notorious for containing a phototoxin. Although this occurrence seems to run counter to current ideas on insect-plant interactions, i.e., specialists are adapted to feed on plants with defensive chemicals whereas generalists are deterred by them (Janzen, 1979), the larval leaf-tying habits of all these species may shade them from the phototoxic effects of hypericin and thus preadapt them for feeding on phototoxic plants (Sandberg and Berenbaum in prep.).

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Notes on the biology of three Riodinine species: *Nymphidium lisimon attenuatum, Phaenochitonia sagaris satnius,* and *Metacharis ptolomaeus* (Lycaenidae: Riodininae)

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Abstract. Observations are presented on the immature biology of three riodinine species from southeast Brazil: *Nymphidium lisimon attenuatum, Phaenochitonia sagaris satnius*, and *Metacharis ptolomaeus. N. lisimon attenuatum* was found to be myrmecophilous while *P. sagaris satnius* larvae inhabit rolled leaves. Based on observations of oviposition behaviour, I suggest that *M. ptolomaeus* larvae are solitary and non myrmecophilous.

The purpose of this paper is to present data on the biology of three riodinine species from southeast Brazil; *Nymphidium lisimon attenuatum* Stichel, *Phaenochitonia sagaris satnius*, (Dalman) and *Metacharis ptolomaeus* (Fabricius). Although these species are not uncommon where found, nothing about their immature biologies has been published to date.

Observations on the first two species were made at Fazenda União, a forest reserve belonging to the Brazilian National Railways at km 140 of the BR101 highway, Rio de Janeiro State. The vegetation is typical of Atlantic tropical lowland forest found in the foothills of the Serra do Mar at about 100 m above sea level. The reserve consists of patches of secondary alternating with areas of primary forest. (fig. 1. *M. ptolomaeus* was recorded from a patch of woods near Barra de São João, an area of transition between the restinga vegetation and the Atlantic forest, described elsewhere. (Callaghan, 1985).

Observations on larval behaviour were made in the field and in the laboratory.

In the following sections, each species is considered separately, with a description of the immature stages followed by a discussion on immature biology.

Nymphidium lisimon attenuatum

Immature stages

Third (?) instar larve (fig. 3): Head light brown. Head, thorax and abdomen covered with short setae. First thoracic segment (T1) with

Fig. 1. Study area at Fazenda União.

Fig. 2. Food plant of *N. lisimon attenuatum*, *Inga* sp.

dark brown dorsal shield and numerous long setae extending cephalad; one lateral spiracle at base of the shield, and two vibratory papillae dorsad beneath edge of the shield. Meso- and meta-thoracic segments (T2, T3) light brown-green mottled. Abdominal segments also light mottled brown-green with a light green irregular band dorsad; spiracles on A1 and A3-A7 ventrally positioned, that on A2 laterally and A8 dorsad and cephalad of the Newcomber's organs. Segments A9 and A10 covered by a dorsal shield with numerous setae around the edge. Head capsul 1 mm; length 10 mm. N = 4.

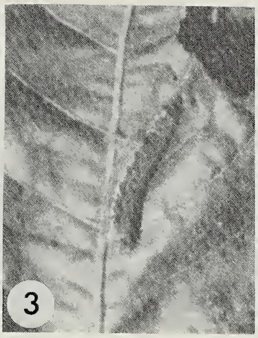

Fig. 3. Third(?) instar larvae of *N. lisimon attenuatum* with ants.

Discussion

Stichel's subspecies *attenuatum* ranges along the coast in southeast Brazil from Santa Catharina north to southern Bahia. Inland it intergrades with subspecies *epiplatea* Butler. *N. l. attenuatum* is found locally in disturbed forest habitats where the males perch in the afternoon along roads and woods edges. They rest under leaves with the body raised 45 degrees from the leaf surface.

The foodplant at Fazenda União was *Inga* sp. (fig. 2), the same genus associated with my other observations of *Nymphidium* biology. (Callaghan, in prep.) The plant has broad pointed leaves with nectaries at the base and grows commonly in open clearings to a height of 2 meters. The *Nymphidium* larvae feed on the newer growth and at nectaries, instead of older, tougher leaves. The larvae are solitary, feeding on separate leaves, a characteristic of other myrmecophilous species. (Callaghan, 1985) In the laboratory the larvae fed at night, remaining motionless on the foodplant during the day.

In the field the larvae were always associated with tiny ants identified as *Wasmannia aropunctata* (Roger, 1863). These gather in large numbers on and around the larva, effectively hiding it from view, thus apparently affording it some protection against predation. Unlike other ants observed with larvae (i.e. *Campanotus* sp., (Callaghan, 1977), *Wasmannia aropunctata* appear very sluggish, not taking an obvious defensive attitude towards intruders. The consequence of this lack of aggressive ant protection was suggested by all 4 collected larvae being found parasitized by ichneumonoid wasps. (Hymenoptera: Trichogrammatidae).

Close observation of larval behaviour with ants indicated that the Newcombers' organs were eversible, protruding outward during the secretion of honeydew. This physiology is similar to that observed in *Menander felsina* larvae. (Callaghan, 1977) No eversible tubercles were observed, such as those found on *Audre* larvae, (pers. obs), nor were the vibratory papillae observed functioning.

Fig. 4. Food plant of *P. sagaris satnius* fam. Melastomataceae.

Phaenochitonia sagaris satnius

Immature stages

Egg: Color white; shaped like a fat tire, diameter 0.8 mm, height 0.4 mm; micropyle 0.2 mm in diameter with many small perforations; covering egg surface is a network of small ridges forming hexagonal patterns with a small protrusion at each intersection. Duration: 12 days. N = 5.

First instar larva: Color uniform light green, except for head which is slightly darker; larve pubescent with two rows of long black dorsal setae on segments T2 to A7; four long, black setae on first thoracic (T1) segment pointing cephalad, long green lateral setae with one black one found on all thoracic and abdominal segments; spiracles observed lateraldorsad on segments A2 through A8. Segments A9, A10 partially covered by a small tail plate. Length 1.7 mm; head capsul 0.3 mm; duration: 9 days.

Second Instar (Fig. 6): Head light brown, face with many short setae. Thorax and abdomen light green with numerous small white dots; T1 with eight long black setae pointing cephalad; segments T2 to A9 with 1 black and 5 long white lateral setae on each side per segment and 2 black dorsal setae; A10 with 4 long black setae around the edge of the tailplate. Length 2.5 mm, head capsul 0.4 mm; duration 8 days. N = 4.

Third Instar: Color and morphology as in second instar, except spiracles outlined in lighter green. Length 3.5 mm; head capsul 0.6 mm; duration: larvae died after 5 days due to unknown causes. N = 4.

Discussion

P. sagaris satnius is the central Brazilian subspecies ranging from the coast of São Paulo north to Bahia then across the Planalto to Mato Grosso. Northward it intergrades with subspecies *iasis* (Godman) and to the south with subspecies *phrygiana* Stichel.

Fig. 5. Ovam of *P. sagaris satnius* inside rolled leaf, part of which has been cut away.

Fig. 6. *P. sagaris satnius* larvae feeding. Note frass chain.

At Fazenda Uniao a lone female was observed ovipositing about 1500 hours on a shrub identified as belonging to the family Melastomataceae. (fig. 4) She alighted on the rolled leaf tube of an unidentified Heterocera larva, walked to the open end and placed a small cluster of five eggs inside the opening. (fig. 5)

Upon hatching, the larvae moved into a folded foodplant leaf provided for them in the laboratory and proceeded to eat the inner side of the leaf, at the same time attaching the upper and lower leaf halves together with silk. During the second and third instars when the larvae were placed on fresh foodplant, they would fold the leaf over by weaving silken threads across the leaf surface, each slightly tauter than the one placed previously until the increased tension slowly drew the halves of the leaf together. These were then secured by numerous filaments between the upper and lower halves, forming chambers inside the folded leaf. The larvae always remained inside, even when feeding, undoubtedly being thus protected from predation.

The larvae always remained together while feeding, lining up side by side in twos or threes. Frass excreted by the larvae stuck together, forming a long chain behind each individual. (fig. 6) Starting two to three days before molting the larvae would cease feeding until a day after molting. At no time was there any evidence of myrmecophilous organs or any behaviour patterns which would suggest their association with ants.

Metacharis ptolomaeus

Immature stages

Egg: Shiny bronze color, 0.5 mm in diameter, 0.2 mm high. Extending from micropile is a network of raised lines forming hexagonal

figures with a protrusion rising at each intersection. Duration: 11 days. N = 1

First instar larva: Newly hatched larva light green, nearly white; pubscent with four long setae extending cephalad from the edge of the prothorax and six equally long setae extending to the rear from the anal plate. Dorsad two rows of setae, a pair to a segment, from T2 to A7, and numerous additional setae extending laterally from the lower edge of each segment. Length 1 mm; head capsule 0.13 mm.

Discussion

M. ptolomaeus inhabits the coast and adjacent mountains in southeast Brazil. It is particularly common in coastal woods and "restinga" vegetation.

A single female was observed ovipositing in a small woods near Barra de São João, Rio de Janeiro State. She laid a single egg at the base of a petiole of a leaf on a small tree identified as *Lacistema* sp. (Flacourtiacea). As no ant species normally associated with myrmecophilous riodinine species were found on the foodplant, and only a single egg was laid, this would suggest that the larvae of *Metacharis ptolomaeus* are solitary but not myrmecophilous. Unfortunately, the larva died before fresh foodplant could be obtained.

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Portable apparatus for photographing genitalic dissections

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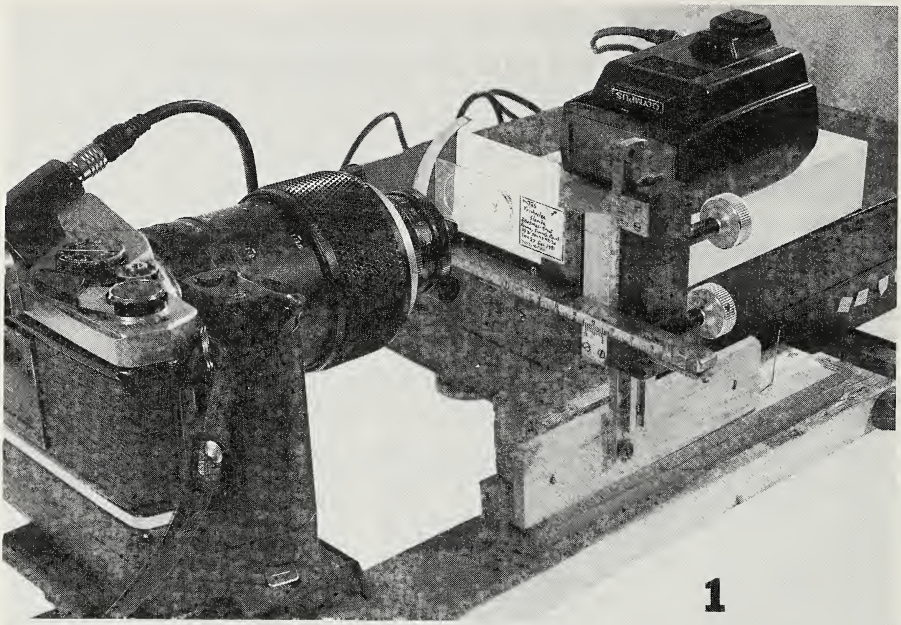
Introduction

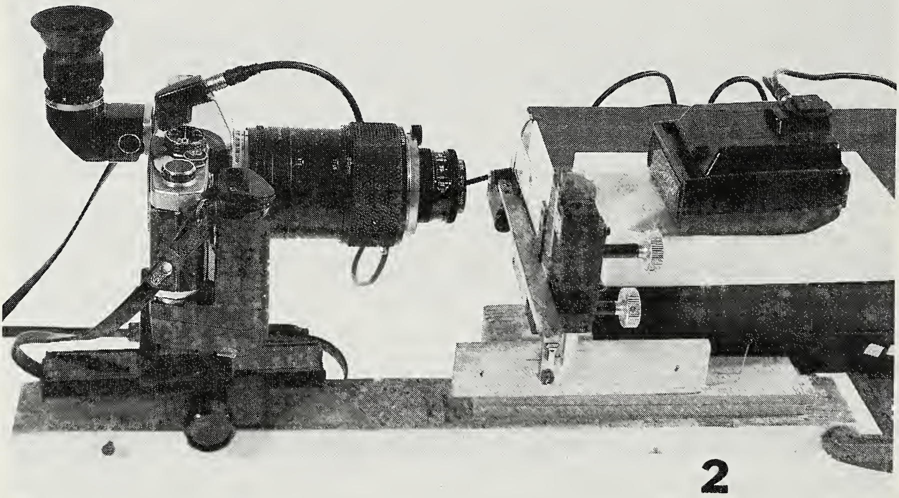
Entomologist's and Lepidopterist's are well aware of the value of genitalic dissections for identifications and comparative morphology. Dissections suitable for photography are time-consuming to produce. Frequently, dozens of slides have to be prepared of a single species to fully understand the range of variation. Every slide ever prepared becomes worth seeing when one is dealing with a problematical species. In addition, species are frequently known from a single specimen which must be borrowed and returned or examined while visiting a museum. Loan institutions are frequently equipped to provide photographs of needed dissections, but this can be a burden on already understaffed collections. The need for quality photographs of dissections is greater than ever.

In recent years, cameras have seen a revolution in sophistication. Of particular note to technical photographers is OTF (off-the-film) light metering and automated flash exposures. This eliminates the chore of calculating flash distances and taking multiple exposures at various F-stops in an attempt to get a properly exposed picture. Lenses made for macrophotography have also improved and dropped in price. Virtually any semitranslucent slide-mounted subject (mouthparts, wings, fleas, etc.) can be photographed by the illustrated set-up (Figs. 1 & 2). Component parts total less than $1,000. A commercially available apparatus would cost over $11,000 (for the Wild M420 Makroskop with the MPS 45/51 Automat, Polaroid CB 101 back and necessary lenses).

Component parts

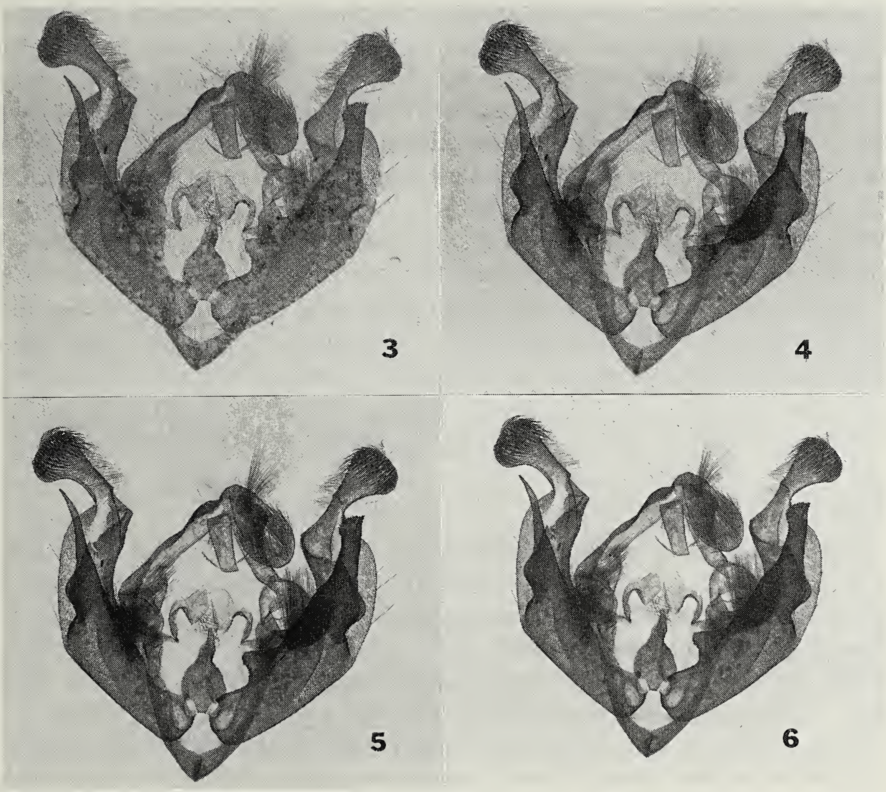
The apparatus described here (Figures 1 & 2) is comprised of (from left to right) 1) an Olympus Varimagni Finder; 2) the OM2n by Olympus; 3) flash-cable coupler with cable attached; 4) self winder; 5) bidirectional monorail from Spiratone; 6) Olympus Telescopic Auto Tube 65-116; 7) objective lens mount (PM-MTob); 8) Zuiko 38 mm Macro F 3.5; 9) salvaged microscope base; 10) opal glass; 11) Olympus T32 flash with blue filter (Electronic Flash Color Filter Set T32 — equivalent to Kodak Wratten 44). The rails are mounted on a board that can be clamped onto the edge of a table. A useful accessory not depicted is an AC adapter that





Figs. 1 & 2. Two views of the photomicrographic set-up.

plugs into the flash eliminating the need for AA batteries. Olympus has removable focusing screens, and a microscope focusing screen (clear field type 1-12) is necessary as the macro lenses require so much light as to make a diffuse focusing screen appear black. The Varimagni Finder can be independently adjusted to accomodate vision defects such as far



Figs. 3-6. Photographs of the same male genitalia slide of **Discestra farnhami** (Lepidoptera: Noctuidae): **3)** Tech Pan, shot at ASA 100; **4)** Panatomic X, shot at ASA 64; **5)** Ilford Pan F, shot at ASA 100; **6)** T-Max 100, shot at ASA 320.

or near-sightedness. The T32 flash is not mounted on the board, but merely supported on a box. The blue filter is placed over the flash to mask the amber color of the Canada balsam commonly used to make the specimen mount. Hardwick (1950; Preparation of slide mounts of lepidopterous genitalia. Can. Entomol. 82:231-235) describes a suitable Lepidoptera genitalia mounting technique. The blue filter makes only a minimal improvement in the resulting picture and the flash can be used without the color filter with only a slight loss in contrast. Of course, the camera can be used without the self-winder. The flash is rested 3-4 inches behind the frosted glass but can be moved closer if full magnification is used on a very thick slide mount. The subject should be at least a quarter inch in front of the opal glass to prevent features of the glass from appearing on the negative. From center to center, the monorail is mounted 7.5 inches from the slide stage to accomodate the entire spectrum for focusing with both the 20 and 38 mm macro lenses. A

38 mm Zuiko MC macro lens is illustrated and I recommend the Zuiko 20 mm MC macro lens for greater magnification. Optimum resolution for the 38 mm lens lies in the 2-6x range; that of the 20 mm lens is 4-12x. This allows full-frame pictures of subjects ranging in width from 2 to 20 mm (40 mm possible by use without extensions. The Zuiko macro lens illustrated is a manual lens. It is now available in automatic (which I recommend). Note, however, that the manual lens uses an adapter (the PM-MTob) which is a universal microscope mount allowing use of compound microscope lenses with this set-up.

Microlepidopterists will frequently have need of even greater magnification than the 20 mm macro offers. Compound microscope lenses that lack an iris have poor depth-of-field capabilities and specialty lenses are required for high magnification. However, an iris attachment can be added to an ordinary microscope lens to greatly enhance depth of focus.

Tips for the best shots

The Olympus Varimagni Finder has a switch allowing one to view at 1.2x or 2.5x. The greater magnification gives better critical focus. If prints appear out of focus, remember that the Varimagni Finder has a focusing ring that must be set for each person without eye-glasses using the same eye each time. I made a white mark to align the focusing ring for my own use after establishing my own critical focusing point.

Stop the macro lens all the way down (f16) for the best depth of field. No loss in resolution was noted at this setting. A shutter release cable (not illustrated) will help prevent vibration during exposure.

Each lens has its own peculiar effect on the camera's ability to autoexpose. I find the best negatives and prints are produced by adjusting the film speed (in the case of Panatomic X, Ilford Pan F, and Tech Pan) one F-stop faster (+1 on the Olympus ASA ring) with the Zuiko 38 mm macro (Figs. 3-5). T-Max 100 was pushed to ASA 320 to obtain the least contrasty print (Fig. 6). If prints appear grainy, it is undoubtedly because of the film. Clean dissections (dust-free surfaces, preparations with minimal debris in mounting medium) are a must, especially for the Lepidoptera genitalia illustrated.

Films

Kodak will soon be replacing its Panatomic X with T-Max 100 (a faster fine-grain film with better tonal range). T-Max 100 sensitivity to the blue filter is 1⅔ stops more sensitive than Pan X. This means the T-Max 100, which has an ASA of 100, will have to be pushed to ASA 320 to obtain the desired low-contrast negative.

Fine-grained films tested include Tech Pan, Ilford Pan F, T-Max 100, and Panatomic X. Tech Pan's ASA is variable according to development (Vetter, J. P. 1984. *In* Richard A. Morton, Ed., Photography for the Scientist, second edit, Academic Press, 393-456), but example given was

taken at ASA 50 to optimize low contrast. Ilford, like T-Max, was affected by the blue filter and will have to be pushed to produce a low contrast negative. Agfa Pan was not tested. Tech Pan had the finest grain (320 lines per mm versus 280 lines per mm in T-Max 100), the lowest contrast, and was the most versatile. The next grade of films, Plus X and others, was much too grainy to be used for this type of photomicrography

Development

The examples (Figs. 3-6) were developed by the following process (only the developing time varies) **1**) Kodak D-76 straight (68°F) for 5 minutes for Panatomic X and Ilford Pan F (8 minutes for Tech Pan and 9 minutes for T-Max 100) (5 seconds agitation every 30 seconds); **2**) Stop Bath for 30 seconds (continuous agitation); **3**) Kodak F-6 Fixer for 5 minutes (continuous agitation); **4**) wash, 1 minute (two changes of tap water); **5**) Perma Wash, 1 minute (continuous agitation); **6**) wash, 1 minute (two changes of tap water); **7**) Photo-flo, 30 seconds; **8**) dry.

Acknowledgements. I thank Christopher Supkis for the pictures of the apparatus and for technical assistance. Mention of brand name is for reference only and does not constitute endorsement of products. Contribution No. 535 of the New York State Science Service.

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Census of the Butterflies of the National Audubon Society's Appleton-Whittell Research Ranch, Elgin, Arizona

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Abstract. The surprisingly rich butterfly fauna of the Audubon Society's Appleton-Whittell Research Ranch is censused and an annotated checklist presented. One hundred and three species are included.

Introduction

The purpose of this study was to inventory and census the butterfly fauna of the Audubon Society's Appleton-Whittell Research Ranch. The Ranch lies approximately 15 km southeast of Elgin in Santa Cruz County, Arizona. The 3170 ha of the Research Ranch were set aside in 1968 by the Appleton family and later acquired by the National Audubon Society. The Ranch serves as a sanctuary for indigenous plants and animals and as a site for non-destructive ecological research. In the 16 years since its founding a great deal of research has been carried out on plants, vertebrates, and the abiotic environment; but little has focused on the invertebrates.

The Research Ranch is comprised of patented (i.e. private), federal (U.S. Forest Service), and State of Arizona parcels. Most of the land is rolling grassland and oak savannah through which small fingers of riparian and pinyon-juniper woodlands extend. The sections of nearly pure grassland in the northern half of the Ranch produced fewer species, and they yielded only a few specialties (species with restricted ranges) not found elsewhere on the property (e.g. *Hesperia uncas lasus*). The deeper canyons toward the center of the Ranch—Post Canyon, Turkey Creek, O'Donnell Creek, etc.—possessed the greatest lepidopteran diversity. This diversity was coupled with a modicum of specialties (e.g. *Amblyscirtes texanae, Adopaeoides prittwitzi*). The extreme southern edge of the Ranch, especially Lyle Canyon and vicinity, had both high diversity and numbers of specialties (e.g. *Yvretta carus, Cyllopsis henshawi*). Proximity to the Huachuca Mtns. is responsible, at least in part, for this.

Methods

A total of 48 visits were made to the Ranch covering 224 hours.

Censusing began in August 1982 and ended January 1984. Most areas were explored on foot during the censuses and some were singled out for special attention. These were: Lyle and Post Canyons, Turkey and O'Donnell Creeks, the higher ridges between these drainages, Finley and Telles Tanks, and the Headquarters area.

Records were organized into ten-day periods. At least one visit was made during each ten-day period for the duration of the study, except for the months of December, January, and February when suitable days (clear, calm, temperatures over 15°C) were uncommon. Numbers of individuals during all visits were tallied for four-hour periods to obtain relative abundances. These were categorized as abundant-A (> 100 per-hour period), common-C (between 13 and 99 per 4-hour period), uncommon-U (between 3 and 12 per 4-hour period), rare-R (1 or 2 per 4-hour period), and single specimen-S (1 per 10-day period. An attempt to tie specific habitats to species occurrence was abandoned because most species have different needs at different times and, depending upon nectaring, water utilization, egg laying, mate location, etc., are found at a number of locations during the lifespan of any given brood or even on any given day. However, certain general distribution patterns were noted.

A reference collection is housed at the Research Ranch Headquarters. An attempt was made to secure a pair of each species (either male and female or a dorsal and ventral view), although this was not always possible. At least one specimen of each "resident" species is represented in the collection. A "resident" species is defined as one which is known or strongly suspected to breed on the Ranch (92 species, 89.3% of total). Included in this category was *Hylephila phyleus*, which probably does not survive winters on the Ranch itself but winters at nearby areas of lower elevation. Nine species (8.7% of total) were designated as "influx" species. These are species of regular occurrence seasonally, but they are unable to survive winters at the Ranch or even in most areas of southeastern Arizona. Eight "influx" species are present in the collection: *Polygonus leo, Urbanus dorantes, Kricogonia lyside, Eurema proterpia, E. boisduvaliana, Phoebis agarithe, P. sennae*, and *Euptoieta hegesia*. One species, *Anteos clorinde,* was seen but could not be netted. The final category, which might be considered a subset of "influx", is the "vagrant". "Vagrant" species do not regularly occur in the area or even in the state but rarely find their way here. They most often appear during and after the chubasco (strong mid and late summer rainy season) season. Two species (1.9%)—*Marpesia petreus* and *Papilio astyalus*—are best classified as "vagrant".

The following annotated checklist mostly follows Miller and Brown (1981), both in sequence and systematics. However, in several cases, for example in generic designations, the older usages of Howe (1975) are preferred.

Discussion

The rich diversity of Lepidoptera at the Ranch, 103 species, is affected by a number of factors. The weather is of primary import, especially winter temperatures and precipitation, prevailing winds, humidity levels, and, especially, summer rainfall. For some of these variables the data were remarkably constant between the two winters of the study (similar winter rainfall totals and low winter temperatures for the two years: 1981-82 vs. 1982-83). The greatest variation occurred during the critical period of the summer chubascos. The onset of these rains was later in 1982 (mid-July) than in 1983 (late June). The total rainfall for the chubasco period—July, August, and September—in 1982 was 20.3 cm, approximately half that for the 1983 chubasco of 39.4 cm. Under a regime of wet weather in Arizona and northern Sonora, Mexico, the vegetation can be conductive to sizeable influxes of primarily tropical species. These conditions existed during 1983 and likely contributed to the rich Lepidoptera activity during that season.

The author's familiarity with local land contours, drainages, plant associations, nectar sources, watering holes, etc. also increased the day-to-day success in the field, accounting for some of the disparity between the two seasons. For example, on August 18th, 29 species were found in 1982 and 49 in 1983.

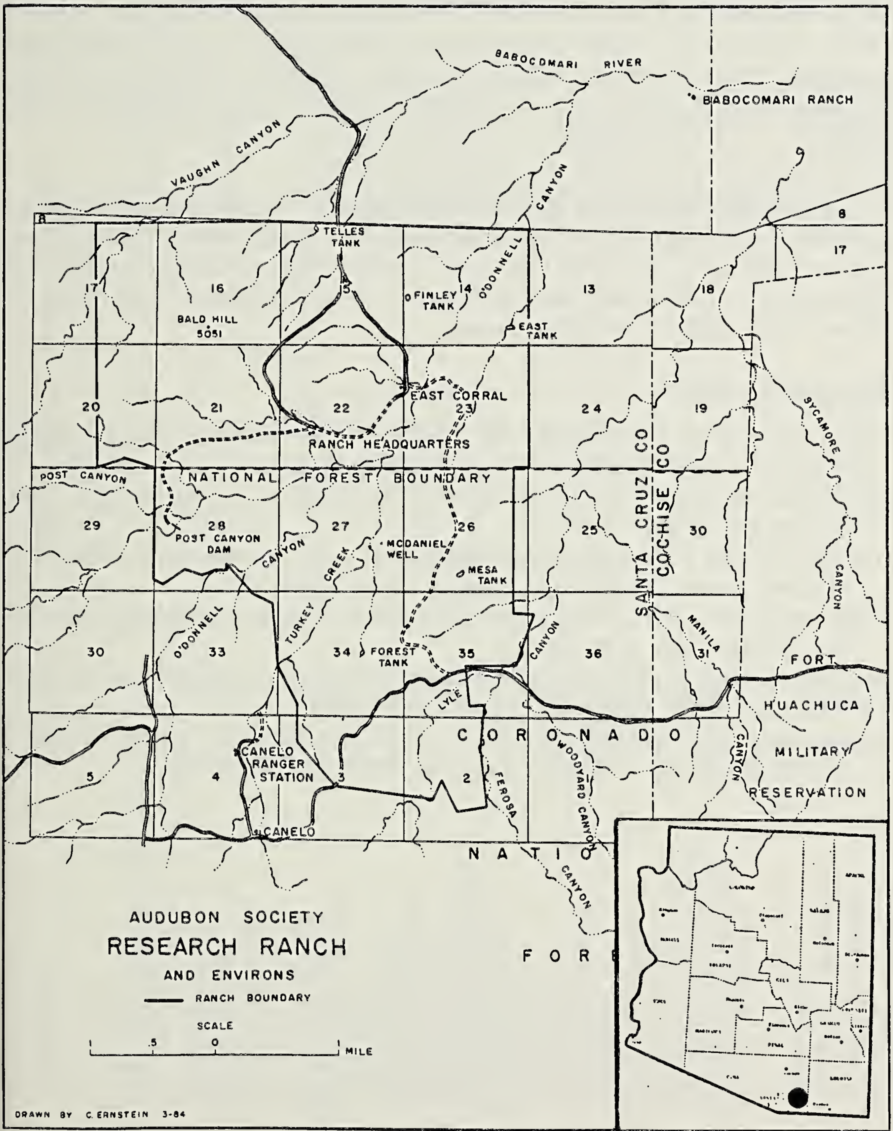
The late rainy season in August and September usually produced the greatest concentrations of individuals and the highest numbers of species (Fig. 1) for the year. During this study, the highest species count for a single trip was made on 2 August 1983 when 51 species were recorded. In fact, the four trips made between 27 July and 3 September in that year produced the four highest counts, all yielding 49 or more species per day. A secondary high was recorded in May 1983 following

Temporal Distribution Month	Average Number Species Per Visit	Total Number species Per Month
January	3.00	3
February	1.33	4
March	14.50	21
April	22.33	35
May	34.25	55
June	31.75	47
July	37.50	59
August	37.83	67
September	37.83	67
October	33.42	57
November	26.50	41
December	3.66	9
Total	—	**103**

Figure 1.

an unusual extended wet period. Under more normal conditions, the May numbers of individuals and species probably would have been more in line with those of April and June.

Lows for numbers of individuals and species were found in December, January, and February when freezing night temperatures were the rule. The lowest temperature of the study (-10.6°C) was recorded on 24 December 1982. Insect activity is low during these months and even lower in the canyon bottoms due to cold air drainage. Those species favoring slopes and ridges have a better chance of maintaining adult populations over the winter (e.g. *Euptoieta claudia*).



A number of other species have been documented from the northern Huachuca Mtns., the Mustang Mtns., Babacomari Cienega, Canelo Cienega, and other locales in the general vicinity of the Research Ranch but failed to turn up during the study. These species include *Systasea zampa* (W.H. Edwards), *Erynnis meridianus* Bell, *Celotes nessus* (W.H. Edwards), *Oarisma edwardsii* (Barnes), *Stinga morrisoni* (W.H. Edwards), *Atrytonopsis deva* (W.H. Edwards), *A. python* (W.H. Edwards), *Amblyscirtes cassus* W.H. Edwards, *A prenda* Evans, *Agathymus evansi* (H. A. Freeman), *Megathymus ursus* Poling, *Incisalia augustus annetteae* dos Passos, *Phaeostrymon alcestis oslari* (Dyar), *Euphilotes rita* (Barnes & McDunnough), *Apodemia palmerii* (W.H. Edwards), *Thessalia fulvia* (W.H. Edwards), *Polygonia satyrus* (W.H. Edwards), *Anaea aidea* (Guerin-Meneville), and *Gyrocheilus patrobas tritonia* (W.H. Edwards). Any records of these or other especies from the Research Ranch property should be reported to the author.

Acknowledgements. The author would like to thank the following for guidance, encouragement, plant determinations, suggestions, map-making, general tidbits, etc.: Jane and Carl Bock, Vern and Nancy Hawthorne, Joe and Helen Taylor, Jack Kaiser, Doug Danforth, Arnold Moorhouse, Char Ernstein, Renee Vitali, and the Audubon Society.

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SPECIES LIST

SPECIES	STATUS	J	F	M	A	M	J	J	A	S	O	N	D	HABITAT	REMARKS
HESPERIIDAE															
Pyrrhopyge araxes arizonae	P								R	U	S			Oak Canyons	9 Oct 1982, latest capture in the state
Polygonus leo	I								S	R					Strong nectarer
Zestusa dorus	P			S	S									Oak hilltops	Lyle Cyn vicinity only
Urbanus dorantes	I							S		S	R	S			Expected more commonly some years
Achalarus casica	P					R	R		R	S				Wooded canyons	
Thorybes pylades	P					U	C	C	C					Wooded cyns	
T. drusius	P							R	R					Wooded cyns	South end of Ranch only
Cogia hippalus	P					U	U	U	C	U				Rocky cyns	Active in the mornings
C. caicus moschus	P				R	R		R	R					Limestone cyns	Double-brooded
Staphylus ceos	P				R	U	R	R	U	R				Shaded thickets	
Erynnis brizo burgessi	P			R	U									Oak hilltops	Also comes to water
E. juvenalis clitus	P							S						Oak cyns	Lyle Cyn, 27 July 1983
E. tristis tatius	P			U	R			R	R	R	S			Oak cyns	Also hilltops
E. funeralis	P				R	R		R	R	R	R	U		Widespread	Males are patrollers
Pyrgus albescens	P				R	U	C	U	U	U	A	A		Widespread	
P. philetas	P				R	U	R	R	R	R	C	R		Dry arroyos	
Pholisora catullus	P							R	R	S				Open areas	Mostly near Headquarters
Piruna mexicana	P								S					Oak canyons	Lyle Cyn, 19 Aug 1983
Copaeodes aurantiaca	P				R	R	R	R	R	U	U	R		Dry arroyos	Males territorial
Adopaeoides prittwitzi	P							R	S					Perm. water	Grass feeder, *Paspalum*. sp.
Hylephila phyleus	P									S	R			Gardens and flowers	Present at the Ranch only in 1982
Yvretta carus	P				S	R		R	R					Grass benches	Lyle Cyn vicinity only
Hesperia uncas lasus	P								R					Open grassland	Present at Ranch only in 1982
H. pahaska williamsi	P				R	R	R		R	R	R	R		Oak grassland	Strong hilltopper
H. viridis	P								S					Oak grassland	Lyle Cyn, 2 Aug 1983
Atalopedes campestris	P					S					R			Grass benches	Lyle Cyn vicinity only

Atrytonopsis lunus	P							R	R					Wooded cyns	Most active mornings
A. pittacus	P				U	U	S				S			Oak grassland	Hilltopper, fall brood is sporadic
A. edwardsi	P					R	R			S				Dry arroyos	Upper altitudinal limits
Amblyscirtes simius	P							R	R					Oak grassland	Hilltopper, SW limits
A. exoteria	P							U	R					Wooded cyns	Most active mornings
A. aenus	P							U	U	S				Cyn hillsides	
A. oslari	P							R	R	S				Open canyons	Scarce statewide
A. texanae	P							S	R					Open canyons	Westernmore populations
A. nereus	P							R	R					Oak grassland	South end of Ranch only
A. nysa	P						S	R	U	S				Rocky arroyos	Males territorial
A. eos	P			R	C	U	R	U	U	R	R			Grassy slopes	Multiple-brooded
Lerodea eufala	P										R			Grassy cyns	At Ranch only in 1982
Agathymus aryxna	P									U	R	S		Oak grassland	Agave association, puddles
PAPILIONIDAE															
Battus philenor	P			S		R	R	U	R	R	R	S		Widespread	May not breed at the Ranch
Papilio polyxenes asterius	P			S		S	S	S	S	R				Hilltops	Wild and cultivated Umbells
P. cresphontes	P					S			R		S			Widespread	May not breed at the Ranch
P. astyalus pallas	S							S						Mexico	Lyle Cyn, 27 July 1983
P. multicaudata	P					S	R	R	R	S				Moist cyns	*Fraxinus* and/or *Prunus*
PIERIDAE															
Pieris protodice	P		S	U	C	C	C	C	U	U	U	R		Open areas	Oviposition on *Descurainea sophia*
P. rapae	P				R					R	R	S		Mostly gardens	Cultivated Cruciferae
Euchloe hyantis lotta	P	S	U	R										Oak grassland	Strong hilltopper
Colias philodice	P										U	R		Open canyons	Relationship with *eurytheme* unclear
C. eurytheme	P	U		U	U	C	C	U	U	U	C	C	R	Widespread	
C. cesonia	P			S	R	U	U	U	U	C	A	C	S	Widespread	
Anteos clorinde nivifera	I									S					Post Cyn, 3 Sept 1983
Phoebis sennae marcellina	I				U	R	S		C	C	C	R			Unidirectional movements apparent
P. agarithe	I									S					Lyle Cyn, 3 Sept 1983

SPECIES LIST

SPECIES	STATU	J	F	M	A	M	J	J	A	S	O	N	D	HABITAT	REMARKS
Kricogonia lyside	I							U							Apparent flight, 27 July 1983
Eurema boisduvaliana	I											S			Turkey Creek, 11 Nov 1983 '
E. mexicana	P				S	U	U	C	U	U	C	C		Widespread	
E. proterpia	I								R	C	U	R			Reestablishes populations most years
E. nicippe	P		S	S	R	U	U	U	U	U	C	C		Widespread	
Nathalis iole	P			R	C	C	C	U	U	U	C	C		Widespread	Flight low to ground
LYCAENIDAE															
Atlides halesus	P			S		S		S	S					Hills, flowers	Mistletoe feeder
Ministrymon leda	P					S	U	C	U	U	U	U		Mesq. grassland	Shade during heat of day
Mitoura siva	P			R	R									Jun. woodland	Post Cyn, Turkey Ck
Strymon melinus	P			U	U	U	U	U	U	R	R	R		Widespread	
Brephidium exilis	P					R	R	R	R	U	R	R	S	Disturbed areas	Mostly Hdqtrs vicinity
Leptotes marina	P					U	C	C	C	C	U		S	Widespread	
Hemiargus ceraunus gyas	P							R	U	U	C	U		Open areas	Damp soil, nectar
H. isola alce	P	S				R	C	C	C	U	C	C	S	Widespread	
Everes comyntas	P				S	R	R	S						Moist cyns	Genitalically determined
Celestrina argiolus cinerea	P						S							Widespread	Post Cyn, 4 June 1983
Icaricia acmon texana	P					R	U	U	U	U	U	U	S	Widespread	
Calephelis nemesis nemesis	P					S				S	R	R		Moist cyns	*Baccharis* association
C. arizonensis	P									R	U	R		Rocky cyns	Turkey Ck, Lyle Cyn
Emesis zela cleis	P			R	R	R		R	U	S				Oak woodland	Double-brooded
E. ares	P								S	R				Oak woodland	Single-brooded
Apodemia mormo mejicanus	P									R				Open grassland	Near *Eriogonum wrighti*
LIBYTHEIDAE															
Libytheana bachmanii larvata	P					S	S	R	R	U	R	R		Widespread	Breeds near Ranch, wanders in

NYMPHALIDAE															
Agraulis vanillae incarnata	P				S					S	R	S		Around Passiflora	May not breed at Ranch
Euptoieta claudia	P		R	R	R	C	A	C	C	C	A	C	S	Open grassland	
E. hegesia hoffmanni	I						S		S						Both records from Lyle Cyn
Poladryas arachne gilensis	P				C	U	U	U	R	U	S			Grass hilltops	*Penstemon* association
Thessalia theona thekla	P				S	U	R	S	R	R	R			Oak grassland	Strong hilltopper
Chlosyne lacinia crocale	P				S	U	U	R	U	U	U			Widespread	Various Compositae
Dymasia dymas chara	P					U					S			Widespread	Most Sonoran Zone habitats
Texola elada perse	P									R	S			Widespread	Present only in 1982
Anthanassa texana texana	P							S		R	R	R		Moist canyons	Avid nectarer
Phyciodes tharos distincta	P					R				R	R			Cienegas, streams	Abundant at nearby areas
P. picta canace	P				S	R	R	R	U		R			Open canyons	Most regular in sacaton flats
Nymphalis antiopa	P			R			S			S	S	S		Perm. water	Willow association
Vanessa virginiensis	P			S		U	U	R	U	U	U	C		Widespread	
V. cardui	P			C	C	C	U	C	U	C	U	C	U	Widespread	
V. annabella	P			S		S					R	S		Widespread	
V. atalanta rubria	P				S	S						S		Wooded cyns	
Junonia coenia	P					U	C	C	C	U	U	U	R	Open canyons	Most active afternoons
J. nigrosuffusa	P	S			R	R	U	U	U	U	U	R		Open canyons	Males territorial
Limenitis arthemis arizonensis	P					R	R	S	R	R	R			Perm. water	Willow association
Limenitis archippus obsoleta	P								S	S				Perm. water	Common at nearby cienegas
Adelpha bredowii eulalia	P					U	U	U	R	U	U	U		Oak canyons	Occasional nectarer
Marpesia petreus	S									S				Mexico	Lyle Cyn, 3 Sept 1983
Cyllopsis pyracmon nabokovi	P									R	R			Wooded cyns	More common at higher elev.
C. henshawi	P						R							Wooded cyns	More common at higher elev.
Megisto rubricata cheneyorum	P					U	A	C	U					Oak grassland	Not known to nectar
Danaus plexippus	P					S				U	R	R		Widespread	Breeds at Canelo
D. gilippus strigosus	P					U	U	C	U	C	C	C		Widespread	Asclepiadaceae feeder

KEY

Status
P = Permanent (breeds at or near the Ranch)
I = Influx (Summer immigrant into area with some regularity)
S = Stray

Abundance
A = Abundant (100 + seen/day at least twice/month)
C = Common (12-99 seen/day at least twice/month)
U = Uncommon (3-12 seen/day at least twice/month)

Notes on a little known ecologically displaced blue, *Agriades pyrenaicus ergane* Higgins (Lycaenidae)

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Abstract. The distribution, ecological relationships, and early stage features of the recently described blue, *Agriades pyrenaicus ergane*, are described. This species is widely disjunct, occurring in the high mountains of northern Spain, Yugoslavia (?), Caucasus, and in a specialized habitat in lowland Ukraine.

Distribution

The recent discovery and description of *Agriades pyrenaicus ergane* in the southeast USSR was surprising for two reasons: this is a well studied and known region and the species represents a wide disjunction in both distance and ecological conditions from the alpine regions of the mountains of northern Spain and Caucasus, while in the Ukr. SSR their habitats are found at an elevation of 200M. The subspecies was originally described from two adult specimens labelled "Voronezh" (Higgins, 1981). These were collected by O. V. Zuravlev near the village of Divnogorje (fig. 1) in June 1980 according to information given in Korshunov (1984), and a series of topotypes given to the Zoological Museum, Biological Institute, Siberian department of the Academy of Science. Later this subspecies was found in the Ukraine by Nekrutenko and Pljushtch (1983) near the village of Efremovka (fig. 1). The latter is its only known locality in the Ukraine.

Adult Behavior

In 1984 and 1985, I made extensive observations of the ecology of the species near Efremovka. The adult insects flew in the latter part of May. The males emerged first on May 9. The last males were observed May 27. The earliest females emerged on May 17 and were last observed on June 1. The mass flight of both sexes was seen between May 19 and 24.

Although common where they are found, the butterflies are extremely localized and specialized. They are concentrated on the steep southern exposure chalk slopes forming the banks of the river Volchja here, as shown in the habitat view in fig. 2. The butterflies do not fly far from their preferred sites and have never been observed further than 50M from their biotopes. Adult preference are weakly eroded depressions, without shrubs or trees, and with a gradient of 30 to 50. This preference

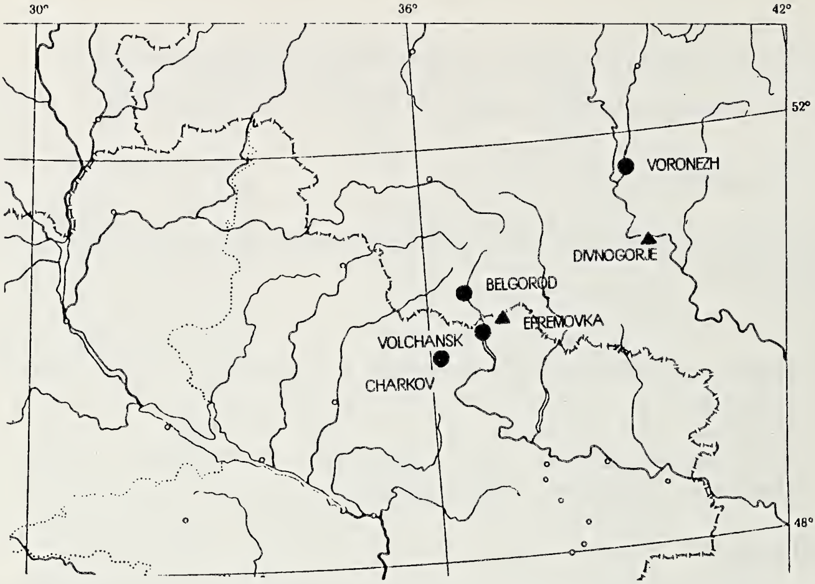

Fig. 1. Map of South East USSR showing cites and two localities of *A. pyrenaicus ergane*.

appears similar to that described by Thomas (1983) for *Lysandra bellargus* in the south of England. Thomas determined that butterfly siting was due to higher temperatures in the depressions, which provided a microclimate more favorable to early stages as well. Fig. 3 shows concentrations of the butterfly hostplant, *Androsace koso-poljanskii* Ovcz. (Primulaceae), which grows in high density in the depressions. Although the plant is occasionally a dominant in its specialized habitat, it is restricted to central Russian chalk hills of the tertiary and is regarded as an endangered plant species, see Zaviruha, Andrienko, and Protopopova (1983: p.35-36). By the same reasoning, *Agriades pyrenaicus ergane* should be regarded as an endangered butterfly. It is both a relict and highly localized.

The development of all stages of the butterfly are intimately associated with its hostplant. The key feature in the emergence of the adults is the flowering time of *Androsace*. Adult butterflies usually nectar on the hostplant and spend some time perching upon it. The females may oviposit on the inner surface of the sepals, among the flower buds, or the inner part of the calyx at the base of the sepals. They also oviposit on the thin stems or in the leaf axils. Before oviposition, the female thoroughly probes with her abdomen, but only single eggs are deposited. Eggs are deposited in a very brief time period (15-60 secs.). Usually the number of females is so large to suitable oviposition substrate that several eggs can be found on one site. Adults also nectar on *Salvia nutans* L., *Linum flavum* L., and other plants which are in flower at the proper time.

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Fig. 2. A chalk uncovering of steep slopes of the south exposition of river Volchja near village Efremovka, Volchanski district, Harkov region, Ukr. SSR—the biotop of the Agriades pyrenaicus ergane.

Fig. 3. The flowering of *Androsace koso-poljanskii* Ovcs. on the chalk slopes.

Fig. 4. The copulating pair of *Agriades pyrenaicus ergane* on its host plant.

Fig. 5. A male *Agriades pyrenaicus ergane* which copulating with fresh but killed female which was being sucked out by a spider. Another male was evidently flirting with this strange pair.

Fig. 6. The female of *A. pyrenaicus ergane* on the flowers of *Salvia nutans* L.

Fig. 7. The caterpillars of *A. pyrenaicus ergane* on *Androsace koso-poljanskii*.

Fig. 8. As 6, different view.

Strong winds and cloud cover do not adversely affect adult flight. They tend to fly within 6 to 15cm of the ground, below serious wind effects. They often perch on stems, chalk stone, and paths. When on the ground they generally rest sideways to the chalk where they are cryptically concealed on the light surfaces.

Both sexes emerge in the daytime, mostly between 1000 and 1410. On a sunny morning adults begin flying at 0730, with males out in mass by 0745. The females follow reaching peak density at 0800. The earliest copulating pair was observed at 0910. The mass of copulation was observed between 1000 and 1500. With the high population densities at the site, as soon as a female emerged, she was seen surrounded by two or three males. Copulation usually started before females would spread their wings.

Prior to their first flight in the morning, adults would open their wings, at a obtuse angle, and turn towards the sun. This apparent thermoregulatory movement lasted several minutes. They would then usually start nectaring at once.

An unusual event was witnessed and recorded (fig. 5) on May 19, 1984. The female of a copulating pair was killed and being fed upon by a spider *Xysticus cristatus (Cl.)* (det: V. E. Gurjanova). The male continued pumping spermatophore while a second male was attempting to interfere, both oblivious to the situation and danger to themselves. Another spider, *Thanatus sp.,* was involved in predation of the blues.

Flight time continued until 1800-1900. The butterflies tended to rest at night at the tops of various low plants, especially showing attraction to the flower stalks of *Salvia nutans* and other flowers with pink or violet colors (fig. 6). The usually grouped in clusters of 3-4, but clusters of 7-8 were seen. At sunrise, the butterflies placed themselves so their folded wings, underside exposed, were perpendicular to the sun.

Early Stages

In the field the egg stage lasts 10-15 days, with a 50% emergence. The remainder collapsed, indicating infertility. The neonate larvae fed exclusively on flower and bud tissue They enter diapause at the end of this instar, while still very small. They move beneath lumps of chalk on or under the soil surface. At this point they effectively disappear from observation.

The following spring diapause breaks with the sprouting of new vegetative growth of the hostplant in early April following snowmelt. Feeding is restricted to young leaves and terminal buds. By the third week in April mature larvae can be found among second and third instars, with larva densities very high. One *Androsace* rosette had 25 larvae (a surface area of about 2 dm^2. A square meter quadrat carried more than 100 larvae. The average density was 8.3 per rosette, or about 6 larvae per dm^2. The larvae, shown in situ in figs. 7 and 8, are cryptically colored and difficult to see among the foliage and blossoms of

Androsace. In the earlier instars they are darker, and usually confine themselves to the top "cone" of the bud where they gnaw through to feed on the internal bud contents. At this time only part of the posterior portion protrudes and is very difficult to detect. The last instar is lighter, and these caterpillars live in a more open situation (figs. 7, 8), usually in groups of three or four. When disturbed they drop to the ground immediately where they remain tightly rolled up for several minutes. The larvae are quite sedentary until time to pupate. They then vigorously move about the hostplant and ground. The first pupation was observed on April 25 in 1985 and was complete on May 1. Pupation from prepupa to eclosion is about 15 days.

Egg: Echinoid, 0.5-0.6mm, grey, with clear micropyle dorsally. Sculpturing of two types, with large, smoother cells dorsally, and smaller more prominently ridged cells laterally. Larva escapes by cutting a hole in the lateral part of the egg.

Larva: (figs. 7, 8). Fourth instar 11-13mm, typical omnisciform. Head completely retractile, small, black. Densely covered with secondary setae. Background color bright green with prominent stripes. Dorsally stripes black with lilac shading with dumb-bell shaped sectors in the middle of each segment, and framed with white. Subdorsal stripes short, thick dark gray extending anterio-dorsal to posterio-ventral on each segment. Subspiracular stripe bicolor; the upper part lilac, the lower white. The pigmentation of the stripes appears epidermal, whereas the background green appears hypodermal. Spiracles round, lined inside in black. Setae on the dorsal margin of spiracles longer, 5-6 times as long as the spiracle diameter.

Pupa: (fig. 9). 9-10mm, strongly sclerotized. Venation of the forewing showing on the integument, this wing cover section slightly raised above the remaining surface. Anterio-ventral part wrinkled. The head protruding with respect to other body parts., antennae, proboscis and legs finely differentiated. Postgenae dark, prominent. Labrum large, heart shaped. Proboscis reaches middle of forewing covers. Pro and mesothoracic legs short, no tarsi visible. Mesothorax strongly protuberant. Eight to tenth abdominal segments ventrally flexed. Cremaster not expressed.

Conservation status Although *Agriades pyrenaicus ergane* is a very abundant butterfly where it occurs, the habitat type is uncommon. It is known from only the two localities in the region of tertiary chalk hills, where its larval hostplant is recognized as a species of concern by its listing the the Red Book of Plants of the USSR. A regular program of monitoring these populations should be instituted formally, and an investigation of ecological requirements started. It is likely similar habitat factors to those regulating populations of *Lysandra bellargus*, as found by Thomas (1983), such as grazing management to keep sward height reduced, may operate here. The large disjunction of this subspecies from its vicariant alpine european and caucasian conspecifics is noteworthy in the argument to study and preserve these unique insects.

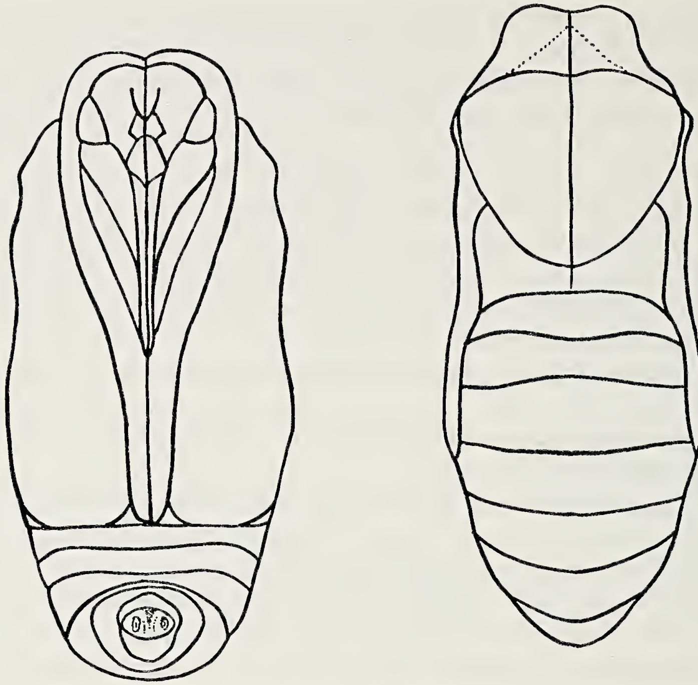

Fig. 9 The pupa of Agriades pyrenaicus ergane.

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Records of *Hypaurotis crysalus* (Edwards) (Lycaenidae) from Western Mexico

The distribution of *Hypaurotis crysalus* (Edwards) in the western United States can be predicted reliably by the range of its larval host, *Quercus gambelii* Nuttall (Fagaceae). Both are widely distributed in the Rocky Mountains from southern Wyoming, Colorado, Utah, and eastern Nevada, south through Arizona and New Mexico. Although the host extends considerably further southward and eastward into Texas and the Mexican states of Sonora, Chihuahua, Coahuila, and northernmost Durango, *H. crysalus* has been reported only once from Mexico (de la Maza and de la Maza, 1975, Rev. Soc. Mex. Lepid. 1(2):64), and this record was from Nuevo Leon.

I have examined two specimens of *H. crysalus* from western Mexico: 1 ♂, Durango, 10 mi W El Salto, 8800', VII-18-64 (J. Powell, Essig Entomological Museum, University of California, Berkeley); and 1 ♂, Durango, Cruz de Piedra, Sierra Madre Mts., IX-4-78 (R. Breedlove, San Diego Natural History Museum). These localities are nearly 900 km south of the international border (Arizona-Sonora). In addition, Richard Holland (personal communication) has collected *H. crysalus* twice in Sonora: 44.9 mi S Huachinera, VII-2-79, 7300'; and 14.8 mi S Huachinera, VII-4-79, 6900'; and Javier de la Maza (personal communication) reports a single specimen from the Sierra San Pedro Martir of northern Baja California.

None of the specimens from Mexico was collected in association with *Q. gambelii*. Holland mentioned that all oaks at the sites of his captures were "encinals" or live oaks; Powell indicated that his speciment was most likely associated with *Quercus sideroxyla* (Humb. and Bonpl.) [= *Q. omissa* (A.D.C.)] (JAP#433; det, J. Tucker); de la Maza's (1975) record from Nuevo Leon is beyond the known eastern range of *Q. gambelii*; and *Q. gambelii* does not occur in Baja California. No species of oak is common to all these regions. The data suggest that the southern limit of *H. crysalus* is not defined by the occurrence of *Q. gambelii*, and that other species of oak must serve as larval foodplants in Mexico.

Comstock (1927, Butterflies of California, pg. 156, published by the author) mentioned the occurrence of *H. crysalus* in California on the basis of three specimens, subsequently believed by Emmel and Emmel (1973, The butterflies of southern California, Nat. Hist. Mus. Los Angeles Co., Sci. Ser. 26:94) to be mislabelled, owing to the absence of *Q. gambelii* in California. However, the record of *H. crysalus* from Baja California suggests that the California records may indeed be valid.

I thank Richard Holland and Javier de La Maza E. for Mexican records of *H. crysalus*; John Tucker (University of California, Davis) for information on *Quercus*; Robert Robbins (United States National Museum) and Jerry Powell (University of California, Berkeley) for comments on the brief manuscript; and Thomas Duncan (University of California, Berkeley) for allowing me access to the Jepson-University of California Herbarium at Berkeley.

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A Chromosome Study of *Brahmaea japonica* Butler (Lepidoptera, Brahmaeidae).

Euroasiatic species of Brahmaeidae present polymorphic populations with an uneven geographic distribution. The disputed taxonomy of this group is also due to the occurrence of populations that show morphological characters intermediate between related species (see fig. 1).

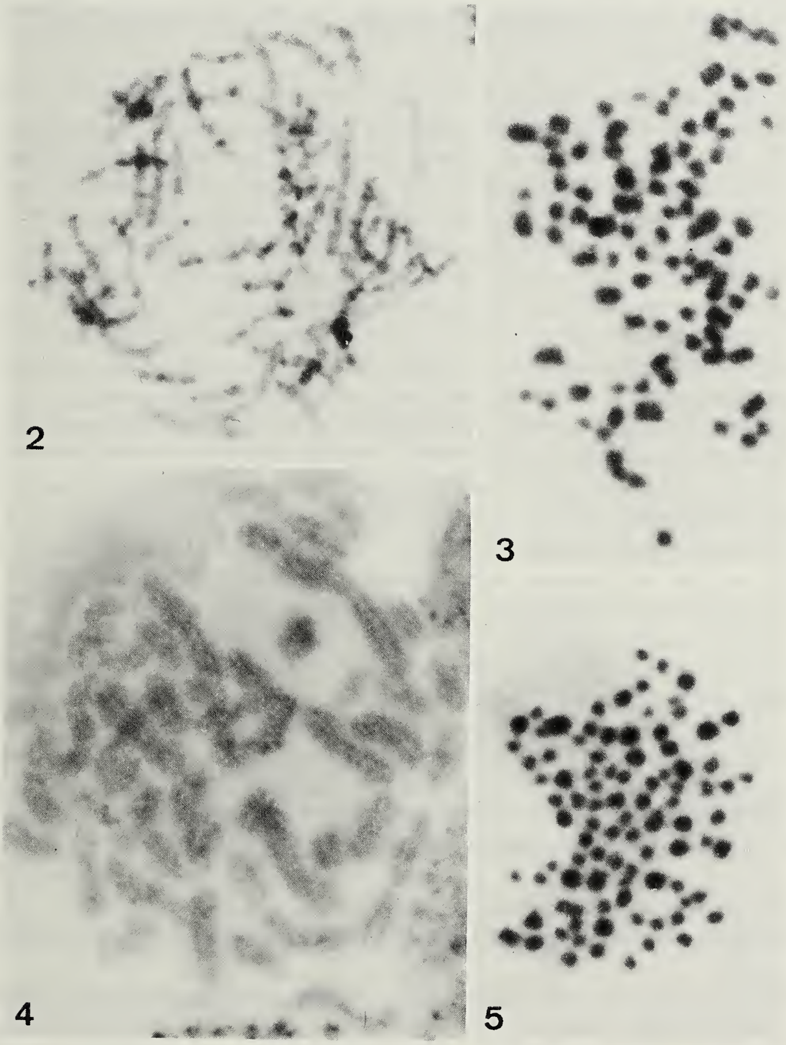
The study of chromosomes could help to explain the affinity among different species. In this regard only *Acanthobrahmaea europaea* Hartig (n = 32, 2n = 64) has been recently investigated (Trentini and Marini, 1985: Atti XIV Congr. naz. ital. Ent.: 299-303).

Fig. 1. Geographic distribution of Brahmaeidae. The data were obtained from papers of Staudinger and Rebel (1901: Friedlander & Sohn Ed., Berlin), Seitz (1911: A. Kernen Verlag, Stuttgart), Mell (1928: A. Kernen Verlag, Stuttgart; 1929: Dtsch. Ent. Z., 5: 337-494; 1937: Dtsch. Ent. Z., 1-19), Rougeot (1971: Masson & Cie Ed., Paris), Chu and Wang (1977: Acta Entomol. Sin., 20: 83-85), Nässig (1980: Nachr. ent. Ver. Apollo, N.F., 1: 77–91), Freina (1982: Entomofauna, 3(9): 129-139), Freina and Witt (1982: Nota lepid., 5 (2-3): 81-85). Euroasiatic species: 1, *Brahmaea certhia* F.; 2, *Brahmeae christophi* Stgr; 3, *Brahmaea ledereri* Rghfr; 4, *Brahmaea porphyria* Chu & Wang; 5, *Calliprogonos miraculosa* Mell; 6, *Acanthobrahmaea europaea* Hertig. Indo-australian species: 7, *Brahmaea hearseyi* White; 8, *Brahmaea wallichi* Gray; 9, *Brahmaea japonica* Butlr. Ethiopian species: 10, *Dactyloceras lucina* Drury; 11, *Dactyloceras ocelligera* Butlr; 12, *Dactyloceras catenigera* Karsch; 13, *Dactyloceras bramarbas Karsch; 14, Dactyloceras barnsi* J. & T.; 15, *Dactyloceras ostentator* Hering; 16, *Dactyloceras Widenmanni* Karsch; 17, *Dactyloceras maculata* Conte.

* Freina (1982: Ibid.) reported a new record of a population of *Brahmaea ledereri* from Hakkari (Turkish Kurdistan region), that shows intermediate features between *B. ledereri* and *B. christophi*; for this reason the author considers *B. christophi* conspecific with *B. ledereri*.

The present research reports the early results obtained on the chromosome set of *Brahmaea japonica*, both males and females.

Brahmaea japonica was reared in 1986-1987 in laboratory on *Ligustrum* sp. and *Syringa vulgaris* from ova received from Japan. Karyological observations were carried out on eight pupae (4 males and 4 females) at one month before adult emergence, employing the air-dried technique (Trentini and Marini, 1986: Genetica, 68: 157-160); the detailed procedure is as follows: after 0.05% colchicine pretreatment for 2 h, testis and ovarioles were dissected out and kept under 1% sodium citrate for 20 min, fixed in 3:1 alcohol-acetic acid, dissociated in 60% acetic acid on a warmed slide, postfixed in Carnoy fluid, and stained with 2% Giemsa (pH 7) for 15-20 min at room temperature.



Figs. 2-5. Spermatogenesis (2, 3) and oogenesis (4, 5) of *Brahmaea japonica*. 2, pachytene; 3, C-metaphase; 4, achiasmatic bivalents; 5, oogonial C-metaphase.

Males. In pupal testes of *Brahmaea japonica* very few mitoses are present probably because the spermatogonial increase occurs in the last two instar larvae. The found C-metaphases show 94 chromosomes; they are rod- and dot-shaped and range from about 0.6 μm to about 2 μm (fig. 3). At the prophase of the first meiotic division 47 bivalents are visible (fig. 2).

Females. Ovarioles still show oogonial mitoses and the start of meiosis. Fifty mitotic C-metaphases of three specimens were scored for chromosome number: five metaphase plates present 2n = 93, forty-three 2n = 94, and two 2n = 95. The chromosomes are rod- and dot-shaped and their length ranges from about 0.7 μm to about 1.5 μm (fig. 5). Some prophases of the first meiotic division with 47 bivalents were observed; they consist of parallely aligned homologues showing their achiasmatic nature (fig. 4), as already reported in other Lepidoptera (Suomalainen, 1965: Chromosoma (Berlin), 16: 166-184; White, 1973: Cambridge Univ. Press).

With regard to the sex chromosome mechanism, the same chromosome number found in both males and females exlcudes an XO system and indicates an XY system, even though the sex chromosomes are undetectable in our preparations.

The only karyologically studied Brahmaeidae species, to our knowledge, are *Acanthobrahmaea europaea* (n = 32; 2n = 64) and *Brahmaea japonica* (n = 47; 2n = 94). The two species are very different in size and wing features, moreover they occur at the extremities of the euroasiatic region. Given the chromosome number 2n = 94 of *B. japonica*, it could be supposed that *B. japonica* presents a quasi-polyploidy (3n − 1) in relation to *A. europaea*. But two facts are contrary to this hypothesis: 1, the chromosomes of *A. europaea* are clearly larger than those of *B. japonica*; and 2, the genome of the two species is about the same size. We think that the variable chromosome numbers in Brahmaeidae are probably due to chromosomal rearrangements (fusion and dissociations), as already reported in other non-parthenogenetic Lepidoptera (Robinson, 1971: Pergamon Press, Oxford; White, 1973: Ibid.).

At a future time it would be valuable to examine the DNA content of both species and the chromosome complements of some other Brahmaeidae.

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Revisional notes on the Genus *Satarupa* Moore (Lepidoptera: Hesperiidae). I. New Synonyms of *Satarupa monbeigi* Oberthür.

Satarupa monbeigi Oberthür, 1921:76, pl. Y, Y bis.
= *Satarupa omeia* Okano, 1982:91-94, Pl. 1, figs. 1, 2 male; fig. 1, male genitalia (**Syn. nov.**)
= *Satarupa lii* Okano and Okano, 1984:124-126, Pl. 9, figs. 1, 2 male; figs. A, male genitalia (**Syn. nov.**)

In 1982, Okano described *Satarupa omeia* from Omeishan, Sichuan, Peoples Republic of China, as a new species. Two years later he described another "new" species, *Satarupa lii* (Okano and Okano, 1984), from exactly the same locality.

We consider both of Okano's two species conspecific with *Satarupa monbeigi* Oberthür, 1921, for the following reasons.

Four described taxa of *Satarupa*, namely *S. valentini* Oberthür, 1921, *S. zulla ouvrardi* Oberthür, 1921, *S. nymphalis khamensis* Alphéraky, 1897 (=*oberthueri* Evans, 1932, =*intermedia* Evans, 1932) and *S. monbeigi* Oberthür, 1921, have hitherto been known from West China (Evans, 1949). Okano should have compared his two species with these four known species, but he neglected to do so. Even if he had no opportunity to examine these species himself or through authoritative persons, he should, at least have keyed his specimens using Evans (1949). Instead, he compared his "new" species with *S. formosibia* Strand, 1927, from Taiwan. In the descriptions he mentioned that *S. omeia* "most closely resemble[d] *S. formosibia* Strand in almost similar appearance", and that *S. lii* was "very near to *Satarupa formosibia* Strand from Formosa". However, he did not mention that *S. formosibia* was the closest species that he compared with those two species among the genus *Satarupa*. Our revisional work (unpublished) suggests that *S. formosibia* is abnormal within this genus in wing markings and male genitalia. Moreover, he did not refer to his own first paper (*S. omeia*) in his second paper (*S. lii*).

We examined two males from the same locality (Omeishan, Sichuan), and determined that those were *S. monbeigi* and so were Okano's two species (based on his figures). In figure 2 of both descriptions, the inner dot in space 7 on the ventral side of the hindwing is vestigial, but still present. Within *Satarupa* the presence of this dot separate the group of species which includes *S. monbeigi* from the group which includes *S. formosibia*. Male genitalia of *S. omeia* and *S. lii* appear slightly different in Okano's figures, especially on the tip of the harpe and the curve of the style. However, these difference appear to be either individual variations or artificial (subjective) modifications of the figures. Figures should be drawn carefully, with sufficient understanding of the structures, rather than rough sketching (Kawazoé, 1973).

We thank J. N. Eliot for examination of specimens in the British Museum (Natural History), S. Miller and A. Kawazoé for review of the manuscript.

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Notes on *Panacea procilla lysimache* (Nymphalidae) from Costa Rica.

The nymphalid butterfly genus *Panacea* is generally thought to range from the highlands of Chiriqui Province of western Panama southward into South American. (DeVries, P.J. 1987. *The Butterflies of Costa Rica and their Natural History*. Princeton University Press, Princeton.) Godman & Salvin (1893) described a single specimen of the genus collected from "Chiriqui" as *P. lysimache* remarking that it was the only specimen known from Central America. In his treatment of *Panacea* Fruhstorfer (1912-1914. *Panacea*. in: A. Seitz (ed.). *The Macrolepidoptera of the World*. Vol. 5, Stuttgart (Alfred Kernan.) downgraded *lysimache* to a subspecies of *P. procilla*, a species that ranges from Panama to the Amazon Basin, and also noted that the holotype of *procilla* remained the only specimen of *Panacea* known from Central America. Until recently I was aware of only four Central American specimens of *P. procilla lysimache*, all from the highlands of Chiriqui in Panama (1200-2000m), and have suggested that the butterfly was likely to be found eventually in Costa Rica from localities in the Cordillera de Talamanca near Panama (DeVries 1987). Here I report the first authentic Costa Rican collection of *P. procilla lysimache* from a forest type very different where it has previously been collected.

On 3 August 1987 at 13:15 hours I collected a fresh male *P. procilla lysimache* (Godman & Salvin, 1893) [forewing length = 45.5mm; proboscis length 24mm] that was feeding at a sap flow on a medium-sized, mature *Persea americana* (Lauraceae) tree growing on the laboratory side of the bridge at Finca La Selva, Heredia Province, Costa Rica. The butterfly was perched head downward about 2m above the ground with the wings open and appressed to the tree trunk and feeding alongside an individual male *Myscelia cyaniris cyaniris* (Doubleday, 1848).

The *P. procilla lysimache* individual was originally noticed at 12:00 hours making sorties around, and perching head downward on the trunk of a introduced Asian tree (*Averrhoa carambolla* : Oxalidaceae), and it may have been feeding on the rotting fruit that littered the ground under the tree. Both trees where the butterfly was observed grew in a open area heavily trafficked by humans located about 30m from the edge of a secondary forest and within 50 m of the Rio Sarapiqui.

While on the wing flutter-glide flight behavior and reddish underside made the *P. procilla* individual appear much like a large *Hamadryas amphinome mexicana* (Lucas, 1853). The following nymphalid species were noted to either be feeding on the fallen fruits of *Averrhoa*, the sap flow of the *P. americana* tree, or flying in the near vicinity at the time of capture: *M. cyaniris*, *Archaeoprepona camilla* (Godman & Salvin, 1884), *A. demophoon gulina* Fruhstorfer, 1904, *Prepona omphale octavia* Fruhstorfer, 1904, *Marpesia merops* (Boisduval, 1836), *Eueides lybia olympia* (Fabricius, 1793), *Cissia hermes* (Fabricius, 1775) and *C. labe* (Butler, 1870). Although I spent a additional 16 days at La Selva, no other *P. procilla* individuals were seen.

There are two considerations I wish to raise regarding *P. procilla* in Central America. One is that Finca La Selva (55-100m elevation) is covered mostly by lowland Atlantic rainforest that is very different from the cloudforests of

Chiriqui where previous Central American records of *P. procilla* originate. The fresh condition of the specimen suggests that rather than immigrating from the mountains of the Cordillera Central or Talamanca, it eclosed either at La Selva or in the immediate vicinity: a broad range of habitats for a rare butterfly species. The second point of consideration is simply to wonder how a large, garrishly colored butterfly species, that is collected commonly near human habitations in South America, has escaped detection in Costa Rica (and Panama) for so many years.

Acknowledgements: I thank N. Greig for asking me "is that a *Hamadryas*?" and running to get my net.

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An Additional Natural Hostplant of *Pieris Virginiensis* (W.H. Edwards) (Pieridae) in Ohio

For many years, the West Virginia white, *Pieris virginiensis* (W.H. Edwards), was known to utilize only toothwort, *Dentaria diphylla* Michx., as a natural hostplant (Klots, 1935). Although other species of *Dentaria* were long suspected to serve as natural hosts (Klots, 1951), only cut-leaved toothwort, *Dentaria laciniata*, was subsequently reported (Shapiro, 1974; Chew, 1980; Cappucino and Kareiva, 1985). Scott (1986) included Pennsylvania bitter cress, *Cardamine pennsyvanica* Muhl., and *Brassica* as hosts without reference. Recently, smooth rock cress, *Arabis laevigata* (Muhl.) Poir., was found to serve as an additional host in central Ohio (Shuey and Peacock, in press). *P. virginiensis* will also feed upon a number of mustards in the lab that are not utilized in nature (Shapiro, 1971; Chew, 1980).

On 25 April 1988, a female *P. virginiensis* was observecd ovipositing on narrow-leaved toothwort, *Dentaria multifida* (Muhl.), on a rich forested stream terrace in Delaware County, Ohio. At this site, *D. laciniata* is abundant and serves as the primary host of *P. virginiensis*. *Arabis laevigata* is also fed upon with some frequency in this area but is uncommon in occurrence. *Dentaria diphylla* is absent. The single ovum deposited in *D. multifida* was collected and reared to pupation on the leaves of this newly discovered host. One additional ovum was later found on *D. multifida* and also reared to pupation.

Throughout its restricted range, *D. multifida* is generally considered uncommon, occurring in Indiana, Ohio, West Virginia, Kentucky, Tennessee, Georgia, Alabama, and North Carolina (Montgomery, 1955; Duncan and Foote, 1975). In Ohio, *D. multifida* is rare and considered threatened. Post-1960 records exist for Delaware, Athens, Washington, and Morgan Counties (McCance and Burns, 1985). The single historical Delaware County site is located several kilometers north of the site found in 1988 (Long, 1956; Allison W. Cusick, pers. comm.). Within Ohio, the known ranges of *D. multifida* and *P. virginiensis* overlap only in Delaware County.

Shapiro (1971) and Chew (1980) noted that *P. virginiensis* females will readily oviposit on many species of mustards but few mustards are typically available in the forested habitats of the butterfly. Hence, the utilization of *D. multifida* in

Delaware County, Ohio is probably due to its presence in an area where *P. virginiensis* is established in association with another, more common *Dentaria*. In the eastern United States, the range of *D. multifida* lies nearly completely within the range of *P. virginiensis* and may serve as a host outside of Ohio.

With the addition of *D. multifida* as a host, *P. virginiensis* has now been found and reared (at least to pupation) on four species of mustards in Ohio. *Dentaria diphylla* and *D. laciniata* appear to serve as the primary hosts, while *Arabis laevigata* and *D. multifida* are known to be utilized locally. An examination of other species of mustards found growing in habitats where *P. virginiensis* occurs will probably reveal additional natural hostplants.

Acknowledgements. Thanks are extended to Reed A. Watkins for his assistance in the field.

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Water pumping in *Lamproptera meges* (Papilionidae)

Lamproptera meges (Zinken), called the "Green dragontail", is a bizarre papilionid resembling a dragonfly in flight. It inhabits the forests and is usually found near running water. It's wingspan is about 4-5.5 cm, and it has 4 cm long tails. The individual shown was photographed on February 28, 1986 in Malaysia, in the middle of the Malayan peninsula west of Cameron Highlands at about 600 m. The behavior shown is extremely unusual because it illustrates water expulsion from the butterfly's anus (Fig. 1). This was a rare synchronization between the 1/250 second shutterspeed and the approximately 1/500 sec projectile-style water squirt. Butterfly was imbibing water from the mud and periodically, about each 4-6 seconds, expelling water. One of the reasons for puddling behavior is the acquisition of sodium ions, as documented in *Papilio glaucus* by Arms, Feeny and Lederhouse (1974. *Science* 185:373-74).

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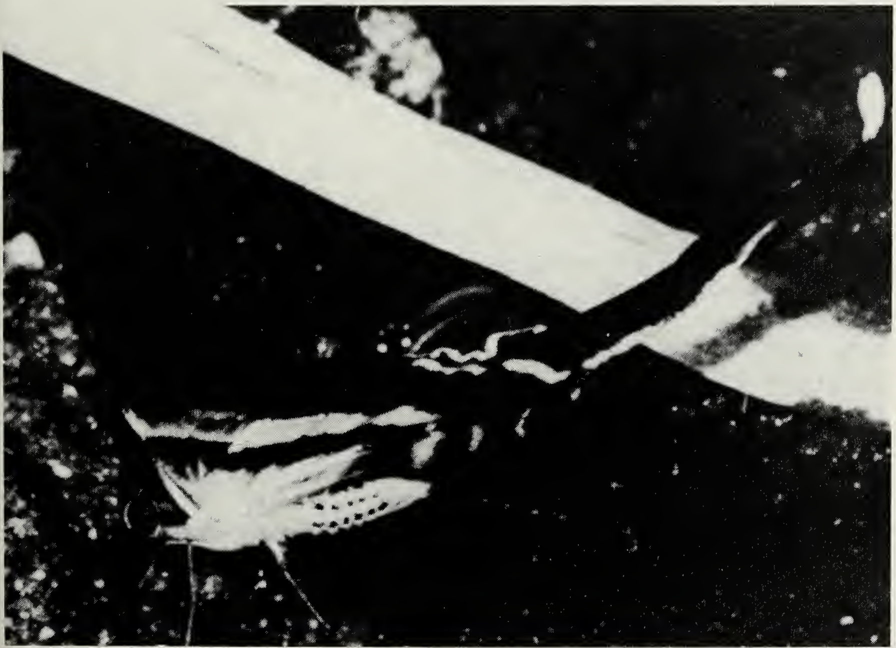

Fig. 1. *Lamproptera meges* expelling water anally. Taken in native habitat, Central Malasia.

Book Reviews

TAGFALTER UND IHRE LEBENSRÄUME. [W. Geiger (Ed.)]. 1987. Schweizerischer Bund für Naturschutz, Basel. 516 pp., col. ill.; ISBN not stated. Price Sfr. 110,—hardback.

The German title (English translation: Butterflies and their habitats) of this book is somewhat misleading: natural history and conservation of Swiss butterflies would have been much better choice. The book has neither a senior author nor editor; this is from a bibliographical and taxonomic points of view inexcusable. 16 authors and editors are listed on p. VI as members of a working group responsible for this book. I propose to attribute the book to W. Geiger (who was obviously the most important editor and author) to avoid future bibliographical confusion. The names of contributors are listed in reversed order, starting with the surname followed by the first name. This too can lead to confusion. Authors of individual chapters are not stated. The book includes the following parts: Biology of butterflies; Butterfly habitats; Decline of butterflies in Switzerland and its causes; Conservation of indigenous butterflies; Systematic part; Distribution and ecology of Swiss butterflies and Glossary. The book is lavishly illustrated in colour throughout the text (adults, eggs, larvae, pupae, habitats etc.) and in addition the adults of all species are illustrated on 25 beautiful colour plates. The species monographs are informative and feature the following topics: description of adults, eggs, larvae and pupae; ecology of adults, eggs, larvae and pupae; Ecology; Distribution (with maps of all species); Phenology and Conservation. To facilitate the identification of some taxonomically difficult species, line drawings of genitalia and some other relevant morphological characters accompany the description, but usually do not reach the very high standard of colour illustrations. The book is extremely well produced and will surely take an important place among the contemporary standard works on the butterflies of Central Europe. It is being offered at a very reasonable price. It is difficult to criticise it except for the confused authorship. I found only a few other minor points of criticism: (1) illustrations of genitalia are somewhat crude, (2) the names of plants are not printed in italics and (3) the short chapter on zoological nomenclature and the subsequent treatment of some names show, that the editors should have asked the advice of a competent taxonomist familiar with English language and the use of the International Code on Zoological Nomenclature (examples of confusion: unavailable names cannot take priority over available names; synonyms do not become unavailable; names proposed for aberrations are always unavailable). It is a great pity that Hesperiidae have been excluded (their exclusion can be justified from a taxonomic point of view, but not in this type of book). I recommend this book to any student of European butterflies and congratulate the team of its authors.

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MARIPOSAS MEXICANAS. Guia para su colecta y determinacion. Roberto de la Maza Ramirez. 1987. Fondo de Cultura Economica, S. A. de C. B., Av. de la Universidad, 975; 03100 Mexico, D. F. 302 pp. 67 color plates. Price $60.00. Hardbound. In Spanish. (Can be ordered directly from Javier de la Maza E., Bochil 340, Col. H. de Padierna, C. P. 14200, Tlalpan, B. F., Mexico.)

This is the first book to provide a comprehensive illustrated introduction to the Mexican Rhopalocera fauna. The writer is a member of one of the most famous lepidopterist families in Mexico, and liberally shares his extensive knowledge of that fauna with us in this magnificently illustrated treatment. With 67 color plates illustrating over 600 species of all families including skippers, it will be an invaluable reference for identifying and collecting a very substantial part of the Mexican butterfly and skipper fauna. In most cases, only the upperside is shown, but these are usually sufficiently diagnostic to allow ready identification of most Mexican species.

A total of 651 species are covered in the text. This is not the entire Mexican butterfly fauna, by any means, nor is the coverage of each species exhaustive, but the volume in total does accomplish its purpose of illustrating and describing many of the most representative species in the country, including taxa described by the very active Mexican lepidopterists from 1950 to date, as well as the well-known endemics such as *Papilio alexiares* (which resembles the Eastern Tiger Swallowtail, *Papilio glaucus*), *Pterourus esperanza*, *Polygonia haroldi*, and many other colorful species in the fascinating Mexican fauna.

The Mexican butterfly fauna is one of the richest and most diverse in the world, and well deserves the further intensive study which this work will help to stimulate. For example, 685 species of skippers alone are known between Guatemala and the United States border, which constitute some 40 to 45% of the diurnal butterfly fauna of Mexico. In the family Riodinidae, some 180 species are found throughout Mexico, 75 species of Pieridae, 56 species of Papilionidae, 6 species of Danaidae, 35 species of Ithomiidae, 70 species of Satyridae, 15 species of Brassolidae, 4 species of Morphidae, 6 species of Acraeidae, 21 species of Heliconiidae, 200 species of true Nymphalidae, 12 species of Apaturidae, 42 species of Charaxidae, 2 species of Libytheidae, and some 230 species of Lycaenidae. There are also at least 10 species known in the Giant Skipper family Megathymidae. Thus the author had a formidable task in selecting the most representative butterflies to both illustrate and briefly describe. The text on each species includes its Latin name, figure reference, habitat description, preferred habitat, and the states (with specific localities following each state name) in which each species occurs. The dates of annual flight period are also indicated for virtually all species.

In addition to the valuable summary of the Mexican butterfly fauna in individual species accounts, de la Maza has an excellent introductory section on the classification of butterflies, fossil butterflies, morphology, life history, genetic phenomena, mimicry and cryptic coloration. An excellent section on collecting, including use of live traps (a very important collecting method in the tropics), the captive culture of butterflies, preparation of specimens, determination and conservation are discussed. The section on spreading specimens is illustrated by beautiful full-color photographs of *Morpho* specimens being spread on a mounting board. One of the most unique features of this book may be the section discussing the butterfly in ancient Mexico, where the representa-

tions of butterflies have been found in archaeological structures and artifacts throughout Mexico. An additionally fascinating section is on the lepidopterology history and some of the chief lepidopterists who have been active in the country. There is an excellent section on habitats and biogeography of the Mexican butterflies illustrated by beautiful color maps and color pictures. In fact, overall the spectacular illustrations and the text makes this one of the best books on the natural history of tropical butterflies that has yet been published. The text is in Spanish, with Latin names for all species. A lepidopterist with a reasonable working knowledge of Spanish will have no trouble in reading the text, which is written in a very informative, smoothly flowing manner. The discussions of abberations, rare species, Monarch migration, and other topics are not overly technical and can be read with ease. The text on the species accounts is sufficiently simple and telegraphic in style that most lepidopterists will be able to translate the habitat, locality, and date information with the aid of a dictionary and no great difficulty, even without a previous knowledge of Spanish.

Overall, this is an outstanding book which should be in the library of every lepidopterist interested in the Mexican fauna and tropical butterflies in general. The inclusion of temperate-zone genera that have reached southward into Mexico in the temperate mountain regions, such as *Polygonia*, will appeal to even North American lepidopterists who are specializing only in the U. S. fauna.

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THE BUTTERFLIES OF INDIANA. 1987 Ernest M. Shull, Indiana University Press, 272 pp. $25.00 U.S.

This volume is the first recent faunal treatment for a entire Great Lakes State. As such, it should be an important library addition for those interested in the region. The book is excellently produced, and is perhaps the most handsome volume on butterflies currently available.

The book is organized into two sections which are subdivided into four parts. Part one includes the introduction and very brief accounts of butterfly biology, collecting, and classification. These are followed by a short discussion of butterfly conservation and the Endangered Species Act. Parts two, three, and four are the species treatments and checklist, which make up the majority of this volume. Each species treatment includes a description of the butterfly, and discussions on status, distribution, habitat, and life cycle. Distribution maps are provided for each species, and all of the species known to occur in Indiana are figured on the 49 plates.

Shull's writing is generally a welcome relief from most terse scientific styles, but some of the text within the species treatments seems irrelevant, especially the recounted observations from Mexico. Most readers will enjoy the species discussions more than the introductory material which because of its brevity, is very telegraphic and choppy. The botanical nomenclature used is erratic, and some plants jump between genera (e.g., shrubby cinquefoil between *Potentilla* and *Dasiphora*).

The forward, by William Eberly, implies that the volume contributes to four areas of butterfly biology; it serves as an identification guide; it contains comprehensive life histories; it contains extensive listings of foodplants; and, it presents much detailed information of the mating habits of butterflies. The following paragraphs assess the attainment of these contributions. My critiques are not intended to be comprehensive, but rather to alert the potential readers of the volume to strengths and weaknesses in Shull's work.

Identification — The plates are of exceptionally high quality and when used with the species descriptions in the text, readily identify most of the species found in Indiana. The treatment of various groups on the plates is very uneven: seven plates figure 53 species of skippers while 15 plates illustrate six species of swallowtails. Some of the specimens figured are too worn to be useful for identification purposes (e.g. *Hemiargus isola* and *Incisalia henrici*). Others are misidentified; *Erynnis juvenalis* appears also as *E. horatius* and *E. lucilius; Incisalia n. niphon* as *I. niphon clarki*; and *Atlides helesus estesi* as *A. h. helesus*.

The treatments of certain subspecies are very problematical, and likely to confuse readers unfamiliar with evolutionary theory. *Cercyonis pegala* is separated into three distinct subspecies (*alope, nephele*, and *olympus*), each with its own text, distribution map, and plate figures. Since Shull demonstrates that these subspecies occur sympatrically, and has even collected them in the same locality on the same day, a more parsimonious solution would have been to accept these "subspecies" as phenotypes of a single species, and simply call it *C. pegala*. A similar problem exists with *Speyeria a. aphrodite* and *S. aphrodite alcestis*.

Life histories — The information presented in the text seems to be a brief recounting of descriptions found throughout the general literature. Although some of the information presented is unattributed, it is never clear if this information is independent conformation of these life histories, or perpetuation of standard (and often incorrect) knowledge.

Foodplants — Again, the information here seems to be recounted out of the general literature (despite the general lack of citations). Most disturbing is the tendency to misrepresent the hosts of the rarer species. For example, *Erynnis persius* is listed as feeding on "willow (*Salix*) and various species of *Populus*", despite the fact that it is restricted to lupine (*Lupinus perenis*) in the lower Great Lakes area. *Lycaeides melissa samuelis* is not considered to be endangered because of the wide "variety of foodplants" that it uses, but in reality, this subspecies feeds exclusively on lupine throughout its range. Most blatantly, *Satyrium edwardsii* is reported to use scrub oak (*Quercus ilicifolia*), a tree that does not occur in Indiana.

Mating habits — This section would be a unique contribution, but unfortunately, very little of the information presented has anything to do with reproductive behavior. The bulk of these discussions are observations made after pairs have coupled, and includes information such as the time of day, air temperature, where the pair was found, where they were resting, and which sex flies in copula. A few brief observations on possible courtship interactions are presented.

One of the more important contributions that treatments of state faunas generally provide, is the resulting set of detailed distribution maps. This volume seems to provide accurate maps for the more common and easily identified species. However, unverified literature records are included without comment on the maps, affectively incorporating all the errors of the past into this volume.

For example, no self respecting *Lethe creola* would ever be lost in a fen in extreme northeastern Indiana (based on a literature sight record). I also suspect that the distributions of many of the skippers reflect erroneous literature records. Some of the more interesting distribution patterns are really a reflection of inadequate collecting: the counties average less than 34 recorded species each.

Readers wanting a general feel for the butterfly fauna of Indiana and adjacent states will certainly find this volume to be valuable. Those interested in more specific information on ecology or hostplants will be less pleased with the text, and will find it difficult to separate the interesting phenomena from the recitations (inaccuracies and all) from the general literature.

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D'ABRERA, B. 1986. Sphingidae Mundi. Hawk moths of the world. E. W. Classey Ltd., 226 pp. 97.50 pounds Sterling.

This is a fantastic pictorial field guide to the taxonomy of the world's Sphingidae. It removes 98% of the taxonomic obstructions to working on or with the ecology, behavior, morphology, etc. of this extremely important group of moths — major pollinators as adults, major food for insectivores as adults and larvae. It photographically figures the adults of about 1,050 species and covers virtually the world fauna. And it should lie at the base of an explosion of biological information about sphinx moths, quite analogous to the production of a field guide to the birds or wildflowers of a region.

There are three roots to the production of Sphingidae Mundi — D'Abrera's fanaticism towards giving us picture books of major lepidoptera groups, Alan Hayes' quarter of a century of organizing our taxonomic knowledge about sphingids, and the British Museum's fanatic attention to the scientific community's need for centralized and curated vouchers for our understanding of animal biology. We were blessed with a mover, a curator, and a responsible repository for the raw material with which they worked. That we should be so forsighted as to cause the juxtaposition of these three items for the other species-rich groups of organisms on this globe, and do it fast enough that guides can appear *now*. And it will be these guides that will provide the taxonomic foundation on which the next half century of conservation and restoration actions will build, actions that will determine what humankind has to work with forever in the tropics.

All taxonomic workers should take note of several traits of this book, many good, a few not so good. First, it is extremely thorough for our knowledge to date, yet obviously does not cover all the sphingids that will finally come to light. Second, the photographs are crystal clear and replace endless pages of unreadable keys, allowing both the novice and the professional to be inspired and construct on this taxonomic base. Third, reams of detailed information about distributions, larval stages, etc. are not necessary to fill the function of guiding the reader to a name, a name that is itself the call number to the book on that species' biology. Fourth, with this table-top summary of a family in hand, immediately a host of ecological, evolutionary, behavioral questions pop to mind

— questions that can now be attacked by those with very little previous knowledge of sphingids or even Lepidoptera; the guide is an obvious magnet for those in other areas of biology. For example, it leaps out from these pages that African *Meganoton, Coelonia* and *Macropoliana* are either congeneric with Neotropical *Manduca*, or we are confronted with the most incredible case of convergence and parallel evolution known in biology; the same applies to the Neotropical *Xylophanes* and the Old World *Hippotion*.

On the debit side of the ledger, I hope that future generators of such guides will view this as a working model, one that can be fine-tuned by collaboration between the users and writers. For example, the inclusion of references to the primary literature on geography and larval (and even adult) biology would at best have added 5–10 pages to the total in the book — such references could be cast in very small type. It is quite possible that Alan Hayes intended to do this before his untimely death. Second, I suspect that there are sphingid workers around the world who could have (would have) quite readily briefly commented on the biology of the species of their area, comments that would have added in the very large amount of current biological information on sphingids that does not appear in the book. For example, it is wondered if *Xylophanes godmani* and *Xylophanes rhodina* are two sexes of the same species (p. 172) when in fact both sexes of both species have been frequently collected in the highlands of Costa Rica in recent years by W. A. Haber, I. Chacón and myself. Third, the reader should have been cautioned that sphingid taxonomy and taxonomic knowledge is still in a state of flux; one can get a very positive identification from this book, but such field determinations should still be checked by someone up on the most recent discoveries in sphingid taxonomy. Fourth, D'Abrera was forced to pick up the production cost out of pocket, in hopes of recuperation through sales; the consequence is a book with a price so great that it will only be purchased by professional lepidopterists and libraries. However, books such as these are of enormous general biological value, and should be widely circulated and available to realize their potential as stimulators of field studies. It is imperative that the general funding community in field science come to recognize that the subsidy of field guidebooks such as this one is as critical as is purchase of field equipment, laboratories, and airplane tickets.

Some readers may object to my calling it a "field guide", owing to its large size and weight. The fact is that the "field" for a worker on sphingids (or any insect group) generally involves both nets and mud, and tables and roofs. This book will have no problems in the library of a biological field station, in a box in the back of a truck, or on a lab bench. The real barrier is cost; expensive books tend to be guarded so carefully that they are not left around for the uninitiated to browse and contemplate.

In sum, any tropical biological station or field research area should have a copy of this book right along with their floras and field guides to vertebrates. We are now at the point of taxonomic understanding for sphingids whereby their biology should be taken fully into account. Lets do it.

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SATURNIIDAE Ecological and behavioral observations of select Attacini. Robert D. Weast. 1989. 53 pp. Published by the author. Available from: SATURNIIDAE, 5324 NW 78 St. Ct., Johnston, Iowa 50131, Price: $16.90

As stated in the author's preface, this book was written by an amateur in an informal style for the non-professional lepidopterist, who makes up the vast majority of the lepidopterists' Society. The book documents attempts to colonize the Des Moines area with *Callosamia promethea, Automeris io,* and *Samia cynthia*; other sections deal with life history data on *Rothschildia* and *Eupackardia*; experiments and general remarks on mating biology and population structure; and a description of a *promethea* X *cynthia* hybrid brood. At the end of several sections the author calls for more research to test various speculations and theories. Amateurs will enjoy the wealth of life history data and will empathize with Weast's enthusiasm and hard work in attempting to better understand Saturniid population biology. I enjoyed the author's humorous accounts of his interactions with the unsuspecting public entitled "Close Encounters of the Other Kind".

Understandably, the professional will find some shortcomings in this work. The book should contain an admonition not to release non-native species into the wild; in Weast's defense it should be mentioned that *promethea* and *io* occur naturally in eastern Iowa and *cynthia* is an introduced exotic not prone to reach pest status on its single introduced host. The mark-recapture data and the Lincoln index calculations are ambiguous. More information about population structure and male mating flight might have been derived by releasing marked individuals and setting out traps according to a standardized grid. Weast could have benefited from a core of student helpers and some professional guidance. I drew two basic conclusions from his population experiments: if an established, stable population shows a 1% survival from ova to adults (2/200 ova survive), then it is not surprizing that one has to release a large number of individuals to establish a colony; secondly, the tentative survival of the *promethea* colony illustrates the ability of Saturniids to survive as low density, dispersed populations.

I believe this small book points out a quandary in the pursuit of Lepidoptera studies by both the amateur and the professional biologist. These two groups need to enter into joint studies. The professional would benefit greatly from the energy and enthusiasm of amateurs and the wealth of life history and other data they collect; the amateur in turn could benefit from the experience of framing important questions, planning appropriate experiments and observations, and evaluating acquired data.

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INSTRUCTIONS TO AUTHORS

Manuscript Format: Two copies *must* be submitted (xeroxed or carbon papered), double-spaced, typed, with wide margins. Number all pages consecutively and put author's name at top right corner of each page. Underline all words where italics are intended. Footnotes, although discouraged, must be typed on a separate sheet. Do not hyphenate words at the right margin. All **measurements** must be metric. Metric altitudes and distances should include imperial equivalents in parenthesis. **Time** must be cited on a 24-hour basis, standard time. Abbreviations must follow common usage. **Dates** should be cited as example: 4. IV. 1979 (day-arabic numeral; month-Roman numeral; year-arabic numeral). Numerals must be used before measurements (5mm) or otherwise up to number ten e.g. (nine butterflies, 12 moths).

Title Page: All papers must have the title, author's name, author's address, and any titular reference and institutional approval reference, all on a separate title page. A **family citation must** be given in parenthesis (Lepidoptera: Hesperiidae) for referencing.

Abstracts and Short Papers: All papers exceeding two typed pages must be accompanied by an abstract of no more than 300 words. An additional summary is not required.

Name Citations and Systematic Works: The first mention of any organism should include the full scientific name with unabbreviated author and year of description. New descriptions should conform to the format: description of male and/or female, type data, diagnosis, distribution, discussion. There **must** be conformity to the current International Code of Zoological Nomenclature. We strongly urge deposition of types in major museums, all type depositories must be cited.

References: All citations in the text must be alphabetically listed under Literature Cited in the format given in recent issues. Abbreviations must conform to the *World List of Scientific Periodicals*. Do not underline periodicals. If four or less references are cited, please cite in body of text not in Literature Cited. Journals and serials not listed in the World List are to be abbreviated according to the Serial Publications on the British Museum (NH), 3rd edition (1980) or given in full.

Tables: Tables should be minimized. Where used, they should be formulated to a size which will reduce to 11 × 19 cm (or 4½ × 7½ inches). Each table should be prepared as a line drawing or typed with heading and explanation on top and footnotes below. Number with Arabic numerals. Both horizontal and vertical rules may be indicated. Complex tables may be reproduced from typescript.

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Development of the Wing Margin in *Precis coenia* (Lepidoptera: Nymphalidae)

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Abstract. The shape of the wings of Lepidoptera is determined in the larval imaginal disk by the position of a peripheral "bordering lacuna". The portion of the imaginal disk proximal to this lacuna (the wing epithelium) will form the wing proper, while cells distal to this lacuna (the peripheral epithelium) undergo programmed cell death during the pupal stage. In *Precis coenia*, cell death in the peripheral epithelium begins on the ventral side by six hours after pupation and gradually spreads throughout the epithelium over the next 72 hours. After this period of cell death the adult wing has achieved its final form and size. The most peripheral of the scale-forming cells on the adult wing become enlarged between 48 and 72 hours after pupation. These scale cells will produce the fringe of long marginal scales. Transplant experiments show that determination of these marginal scales must have occurred prior to pupation, and thus well prior to the period of cell death in the peripheral epithelium. We found that in *P. coenia* the marginal scales do not form a discrete size group but rather are the extremes of a gradient in scale size that extends in from the wing margin for at least 3 scale-cell rows. We postulate that some special property of the wing margin, presumably originating from the bordering lacuna but decaying with distance, is responsible for inducing the formation of the unusually large scales that form the marginal fringe.

Introduction

The wings of butterflies and moths develop during the larval stage as internal imaginal disks. The wing disks undergo a substantial amount of morphological differentiation during late larval life, so that by the middle of the last larval instar they are usually readily identifiable as miniature wings complete with a primitive venation pattern (Nijhout, 1985). The wing veins develop initially as a system of lacunae between the dorsal and ventral epidermal layers of the wing disk. These lacunae radiate out from the base of the wing disk in a branching pattern that presages the future wing venation. In addition, a peripheral bordering lacuna develops, that runs roughly parallel to the margin of the disk. Suffert (1929) showed that this bordering lacuna marks the position of the future margin of the adult wing. During the pupal stage all cells

peripheral to the bordering lacuna disappear and only the portion of the imaginal disk within the periphery of the bordering lacuna will become the wing of the adult. As a consequence, the size and shape of the adult wing is determined by the position and path of the bordering lacuna within the wing imaginal disk. The fine features of the wing shape, such as tails in papilionids and saturniids, as well as the gross morphology of the wing are determined by the path of the bordering lacuna (Suffert, 1929), and any change in wing shape, whether developmental or evolutionary, must have its basis in an alteration of the shape of the bordering lacuna.

Thus we can think of the adult wing shape as being produced by a cookie-cutter-like mechanism that outlines the precise form of the adult wing within the much larger wing imaginal disk. The margin of the adult wing is not the margin of the imaginal disk, and this has several implications when we think about structure and function at the wing margin. It makes us wonder about the morphology of the adult wing edge; about whether and how the dorsal and ventral wing surfaces become reattached at their periphery after death of the tissue distal to the bordering lacuna. It draws our attention to the fact that the margin of the adult wing is further "specialized" in that it bears a distinctive fringe of marginal scales. In most species these marginal scales are much larger, and very different in shape and color from the scales that deck the rest of the wing surface. Thus scale morphogenesis must be under a different type of control at the wing margin than elsewhere on the wing. Moreover, the wing margin appears to have an additional functional specialization. It is clear that the margin is involved in the determination of several elements of the wing's color pattern (Nijhout and Grunert, 1988), and the bordering lacuna provides an obvious structural feature that could be the source of the requisite inductive signal(s).

The present paper reports on a morphological study of cell death at the wing margin of the Buckeye butterfly, *Precis coenia*. We document the spatial and temporal pattern of cell death, the structure of the new wing margin, and the fact that the specialized fringe of marginal scales appears to be induced by a special property of the bordering lacuna at sometime prior to pupation.

Materials and Methods

Larvae of *Precis coenia* were reared at a constant temperature of 27 degrees Celsius on an artificial diet as described by Nijhout (1980a). Microscopy was done on material embedded in JB-4 Resin (Polysciences), sectioned at a thickness of 1 um, and stained with Lee's methylene blue-basic fuchsin (Polysciences). Cell death was determined by uptake of trypan blue according to the method of Humason (1979).

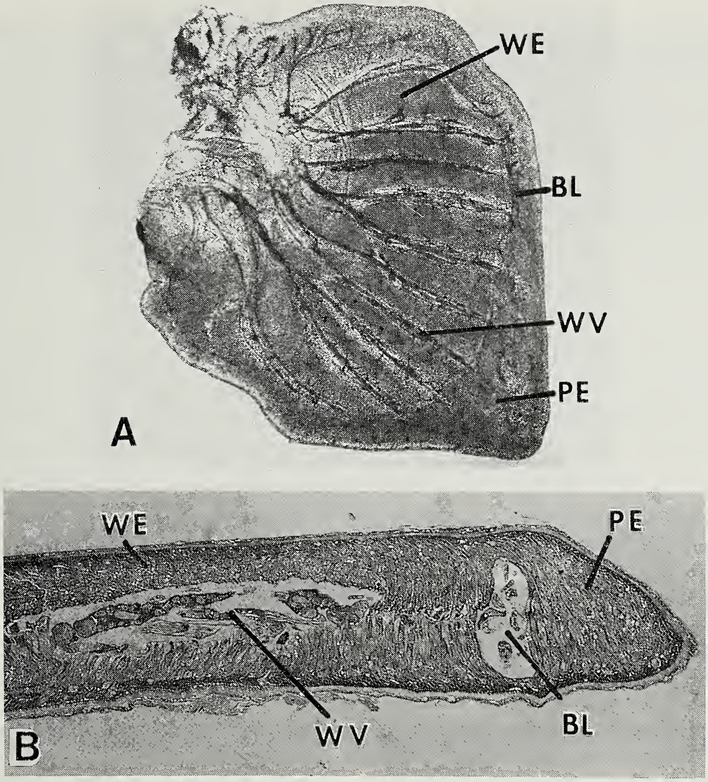

Fig. 1. A. Wholemount of imaginal disk of forewing of *Precis coenia* at day 5 of the last larval instar, and about 2 days prior to pupation. B. Crossection of distal portion of wing imaginal disk at day 5 of the last larval instar. *BL*, bordering lacuna; *WV*, lacuna of wing vein; *PE*, peripheral epithelium; *WE*, wing epithelium. Scale bar is 0.5 mm.

Specimens for scanning electron microscopy (SEM) were air-dried, coated with gold-palladium, and examined and photographed with a JEOL T20 electron microscope.

Results

At the time of pupation the wing has two surfaces each of which is an epithelial cell layer of columnar, tightly packed cells. These surfaces meet and are continuous at the periphery so that the wing's structure resembles a flat bag. The shape of the adult wing is marked by a peripheral lacuna (Fig. 1) which runs roughly parallel to the margin of the disk (Nijhout, 1985). The results presented below will show that this bordering lacuna divides the wing surface into a "*distal epithelium*" which is located distal to the lacuna and which will die during development, and a "*wing epithelium*" which will form the adult wing (Fig. 1).

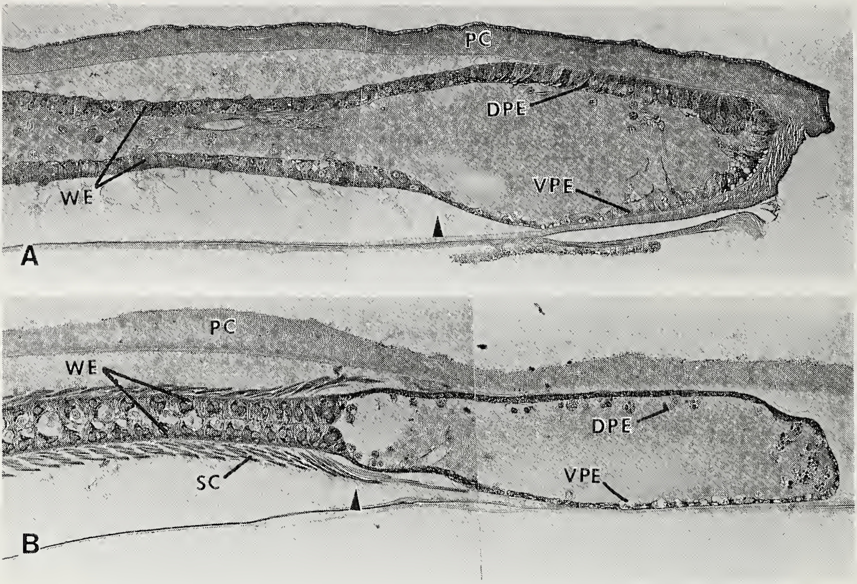

Fig. 2. A. Crossection of pupal wing at 48 hours after pupation. B. Crossection of pupal wing at 72 hours after pupation. Former position of bordering lacuna is shown by arrow. *PC*, pupal cuticle; *SC*, scales of the adult wing; *VPE*, ventral peripheral epithelium; *DPE*, dorsal peripheral epithelium; *WE*, wing epithelium.

Six hours after pupation the dorsal and ventral epithelial cell layers of the pupal wing had separated and surrounded a space filled with hemolymph and free-floating hemocytes. Although the bordering lacuna was no longer discernable, due to the separation of the two cell layers, its former position was still marked by the fact that the cells formerly distal to the lacuna, the distal epithelium, were slightly smaller and thinner than those of the wing epithelium. The boundary between these two cell populations formed a distinct "line" in the wing epidermis. Further studies showed that this line now defined the position of the future wing edge. Trypan blue staining revealed that at this time cells in the ventral part of the distal epithelium had already started to die. Cell death began along the former position of the lacuna and spread distally into the ventral distal epithelium. Cell thickness and cell density in the ventral distal epithelium decreased gradually over the next 48 hours.

At 48 hours after pupation cell death had progressed to the dorsal part of the distal epithelium. At this time the hemolymph space within the pupal wing was gradually diminishing in volume and the dorsal and ventral epithelia in the proximal region of the wing had already become fused Fig. 2A). At 72 hours after pupation the dorsal and ventral epithelia of the wing-proper were once more tightly apposed, and scales

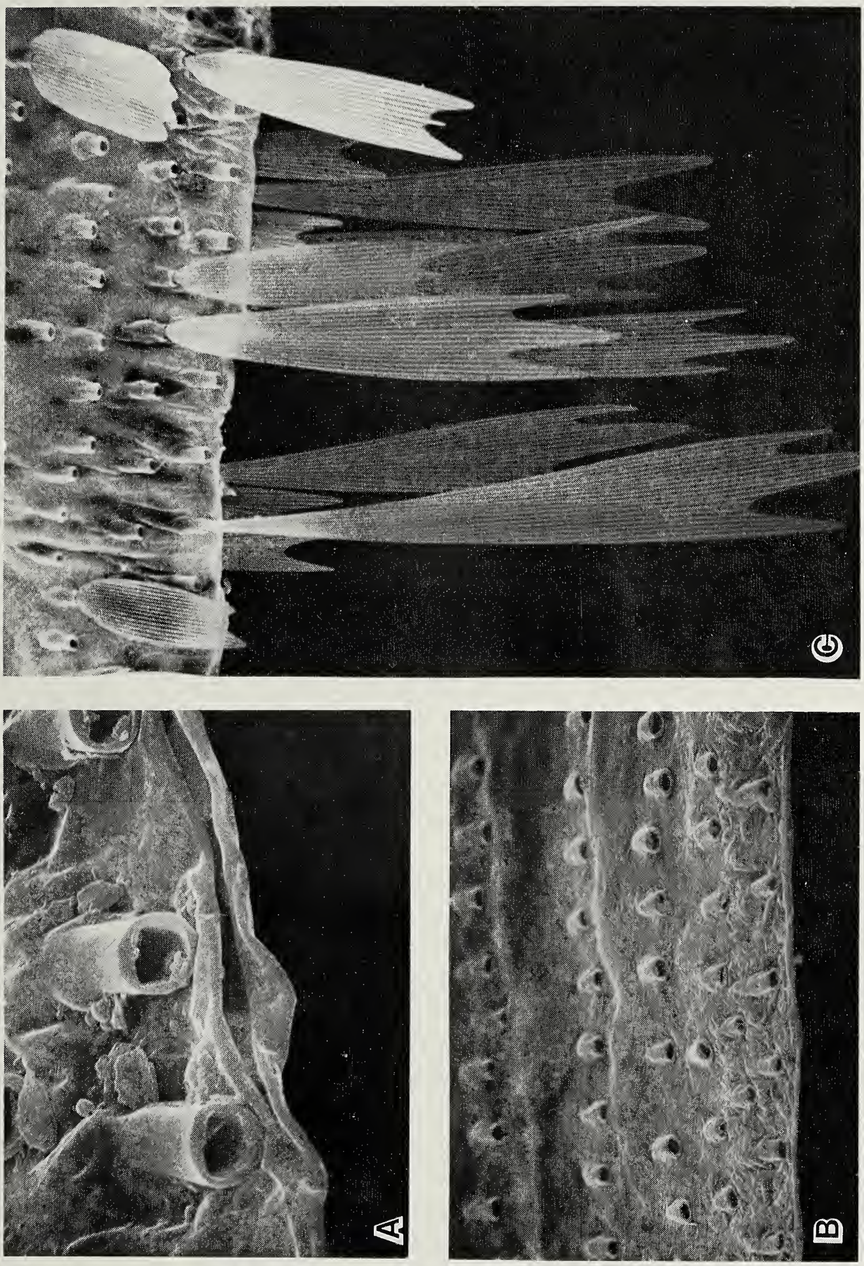

Fig. 3. Scanning electron micrographs of wing margin of adult wing. A. Edge-on view showing separation of dorsal and ventral cuticles. B. View of edge showing parallel rows of sockets of scale cells. C. View of wing margin, with a portion of scales removed, showing gradual increase in scale length with proximity to wing margin.

were in the process of formation (Nijhout, 1980b). In contrast, the dorsal and ventral parts of the distal epithelium did not become fused but remained as a thin bag-like rim around the wing (Fig. 2B). Furthermore, no enlarged scale forming cells were detectable among the surviving cell population in this peripheral epidermis, and no scales were formed in this part of the wing. The scale-forming cells at the very margin of the wing were slightly larger, and had slightly larger nuclei than those of the generalized wing epidermis. This specialization is in accord with the presumptive relation between ploidy level and scale size (Henke and Pohley, 1952).

Since the peripheral tissue of the imaginal disk undergoes cell death, no closure exists between the dorsal and ventral epidermis at the periphery of the developing adult wing. We investigated the morphology of the adult wing margin by scanning electron microscopy, and found that the dorsal and ventral cuticles never fuse but become simply appressed. The absence of fusion between the dorsal and ventral cuticles is shown by the presence of a split which separates both surfaces and which runs at or very near the wing margin Fig. 3A).

As Fig. 3B shows, the scale forming cells are arranged in straight parallel rows which take their course roughly parallel to the wing margin. We found that contrary to initial expectations there was no uniquely differentiated fringe of marginal scales. Instead the size of the scales, and the degree of indentation of their apical margin, increased gradually with proximity to the wing margin (Fig. 3C). Scales which were close to the margin were much larger than scales further inside the wing. Figure 4 shows that the size of the scales decreases exponentially with distance from the margin.

In order to determine whether cells of the peripheral epithelium were already programmed to undergo cell death at the time of pupation, we excised strips of epithelium extending across the bordering lacuna and thus consisting of both distal and wing epithelium from pupae two hours after pupation. These strips were rotated 180° and grafted back in their original site. Thus in these grafts cells of the peripheral epithelium were now placed within the wing epithelium and vice versa. The results of such a graft are shown in Fig. 5. We found that the cells of the grafted tissue always developed according to their original fate. Cells of the peripheral epithelium underwent normal cell death, occasionally leaving a hole in the wing epithelium at the site they were grafted. Most frequently, however, the epithelium contracted around the wound site, as in Fig. 5, and no hole was evident in the area where the peripheral epithelium died. Cells of the wing epithelium survived and when placed so that they could establish continuity with the rest of the wing epithelium they were retained in the adult wing. These grafts retained their original polarity as indicated by the orientation of the scales (Fig. 5). Furthermore, large marginal scales were formed at the edge of the grafted wing epithelium, extending into the space left in the wing by death of the transplanted peripheral epithelial cells.

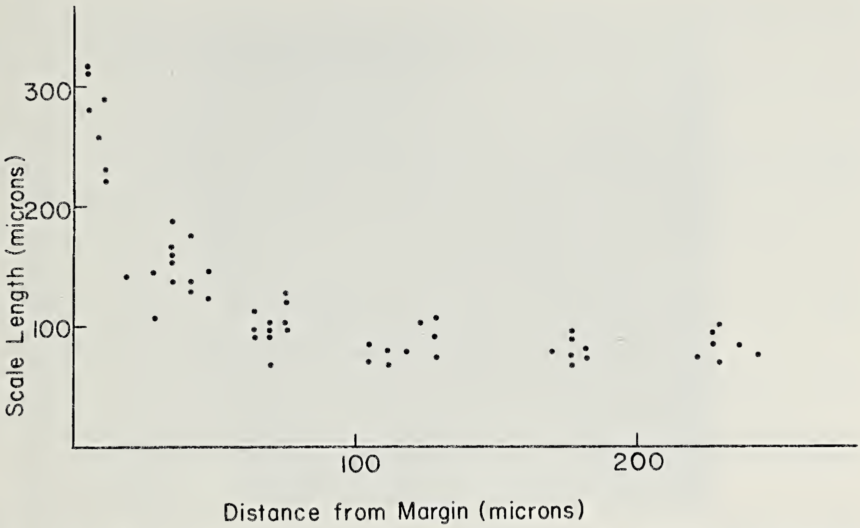

Fig. 4. Graph of scale length as a function of proximity to wing margin. Position of each scale was measured from the the aperture of its socket to the margin.

Discussion

The development of the adult wing of *Precis coenia* is a process with striking morphological changes during pupal stage. As illustrated by Figs.1 and 2 the wing starts as a flat bag-like shape. At the time of pupation it goes through a stage at which the dorsal and ventral cell layers become separated by a voluminous hemolymph-filled space. This separation coincides with the peak of mitotic activity and the later stages of color pattern determination in the wing epidermis (Nijhout, 1980b; Nijhout and Grunert, 1988). After the end of the mitotic period, about 36-48 hr after pupation (Nijhout, 1980b), the dorsal and ventral wing epithelia become closely appressed again but the distal epithelia never fuse. Instead, they form a fluid filled bag-like rim around the entire wing disk (Fig. 2B). Cell death in this peripheral epithelium begins by 6 hours after pupation and continues until at 96 h after pupation the bag-like rim has completely vanished. Thus it is not until the 4th day after pupation that the shape of the adult wing is evident.

Grafting experiments (Fig. 5) show that at two hours after pupation the cells of the distal epithelium are already programmed to die in the course of the pupal stage. The polarity of the scale forming cells has also been determined by this time, as was previously shown by Nijhout (1980a).

Determination of the elongated marginal scales has also occurred by two hours after pupation, since these scales developed normally on transplanted wing margins. Thus determination of the characteristics of the wing margin, including its position, fate of the peripheral

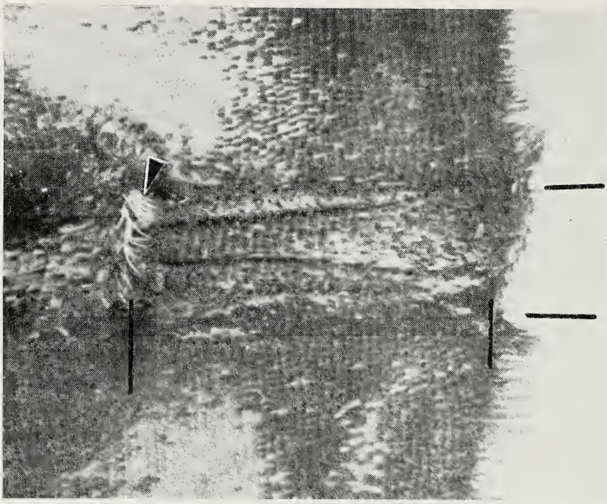

Fig. 5. Result of a grafting experiment in which a strip of pupal epidermis was excised, rotated 180 degrees, and reimplanted so that the former wing margin was now located well within the field of the wing proper. Lines at right and bottom show the limits of the graft. Arrow indicates the position of long marginal scales at the edge of the graft. In this specimen the wing epidermis has contracted and closed off the 'hole' left by the degenerated peripheral epidermis.

epithelium, and character of the marginal scales must have taken place prior to pupation. The fact that cell death in the peripheral epithelium begins at the former location of the bordering lacuna, as well as the existence of the gradient of scale size in the wing epithelium, suggest that the bordering lacuna not only serves as a demarcation between wing and peripheral epithelium but may also have an active role in inducing these two modes of cell differentiation.

The exponential increase in size of the marginal scales with proximity to the margin strongly suggests that a gradient of some sort is a determining factor. The transition from normal scales to very long marginal scales occurs over the course of 3 scale rows, or a distance of about 80 um on the adult wing. But the adult wing of *P. coenia* is expanded by a factor of about 2 from the size of the wing in the pupal stage; thus the actual distance over which marginal cell determination gradient extends on the pupal wing is approximately 40 um. These findings add to the body of evidence that the bordering lacuna in the wings disks of Lepidoptera plays specific and important roles in the development of the wing. Not only does it control the ultimate size and shape of the wing by outlining the areas that will undergo programmed cell death, but it also appears to possess special properties that are involved in the induction of certain elements of the color pattern (Nijhout and Grunert, 1988) and in the induction of marginal scale differentiation.

Acknowledgements. This work was supported by Grant DCB-8517210 from the National Science Foundation.

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The Morpho-Species Concept of *Euphyes dion* with the Description of a New Species (Hesperiidae).

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Abstract. *Euphyes alabamae* (Lindsey, 1923) and *Euphyes macguirei* (Freeman, 1975) fall within the normal range of variation of *Euphyes dion* (Edwards, 1879), and are reduced to synonyms of *E. dion*. The type series of *E. macguirei* probably resulted from unique rearing conditions; no specimens fitting the original description of this taxon have ever been collected in the wild. *Euphyes alabamae* is at best a weakly defined subspecies in which one of the many phenotypes of *E. dion* if fairly stable. A unique *Euphyes* population from Bay St. Louis, Mississippi, differs subtly, but consistently, from all *E. dion* populations and is described as *Euphyes bayensis* new species. Preliminary biological evidence suggests that the new species differs from *E. dion* in habitat requirements and hostplant choice.

Introduction

The genus *Euphyes* is distributed through most of the western hemisphere and contains approximately 20 species. The genus is composed of four well defined species groups (Shuey, 1986) which differ primarily in the configuration of the female genitalia. The *dion* group contains six species level taxa (*E. dion* [Edwards], *E. dukesi* [Lindsey], *E. macguirei* Freeman, *E. pilatka* [Edwards], *E. berryi* [Bell], and *E. conspicua* [Edwards]), all of which are confined to wetland habitats. An additional taxon, *E. alabamae* (Lindsey), is usually considered a subspecies of *E. dion*, but often has been placed as a distinct species (e.g., Clark and Clark, 1951; Forbes, 1960; Miller and Brown, 1981). Because of their restricted habitat requirements, these species are localized and among the least collected skippers in eastern North America.

The *dion* group (sensu Shuey, 1986) contains two problematic names which refer to taxa of uncertain status, *E. alabamae* as mentioned previously, and *E. macguirei*, which has remained an enigma to most lepidopterists since its recent description. The resolution of these taxa's status has been hampered by their relative rarity and the difficulty of amassing sufficiently long series to investigate interspecific variation. My purpose is to briefly examine the status of the two problematic taxa, and to describe a new species from southern Mississippi.

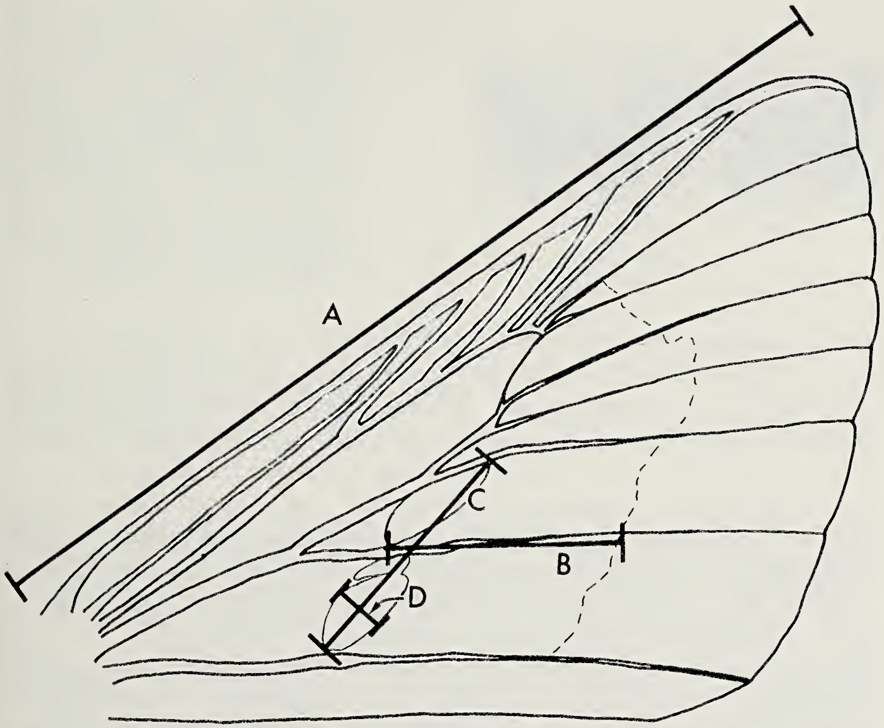


Fig. 1. Wing measurements recorded; A — wing length; B — extent of orange pattern along vein V_2; C — stigma length; and, D — stigma width.

Materials and Methods

I examined material of all the *dion* group species. Particulary relevant material included several hundred specimens of the *dion/alabamae* complex from throughout eastern and central North America; the holotype male of *E. alabamae*; the holotype male and allotype female of *E. macguirei*; and a series of 32 males and nine females of an undescribed taxon from southern Mississippi.

For wing pattern analysis, 20 males and 20 females were randomly selected from series of the *dion/alabamae* complex from Ohio+Indiana and Mississippi and the undescribed taxon (only nine females of this taxon were available). Characters measured (Fig. 1) with an ocular grid included forewing costa length (to the nearest 1/2mm), extent of the orange pattern along vein V_2 (to the nearest 1 4mm), stigma length (to the nearest 1/4mm), and stigma width (to the nearest 1/8mm).

PROBLEMATIC NAMES

Euphyes macguirei Freeman, 1975. This taxon was described from a short series (four males and one female) of reared specimens from Benbrook Reservoir, Tarrant Co., Texas. Although Miller and Brown

Fig. 2. *Euphyes macguirei*—like adults reared from Logan Co., Ohio ova. Both specimens were reared on poor quality cuttings of *Carex lacustris*. Similarities to *E. macguirei* include small size (forewing length 15 mm and 14.5 mm respectively), and reduced orange pattern elements.

(1981) accepted this taxon as a valid species, most lepidopterists have been skeptical about its status, presumably because of the unique circumstances surrounding all of the known specimens and their similarity to *E. dion*. This is probably the only butterfly in North America which has never been captured; all specimens known to me have been reared. Freeman (1975) listed five characteristics which separated. *E. macguirei* from *E. dion*. Unfortunately, none of these characteristics can withstand close scrutiny.

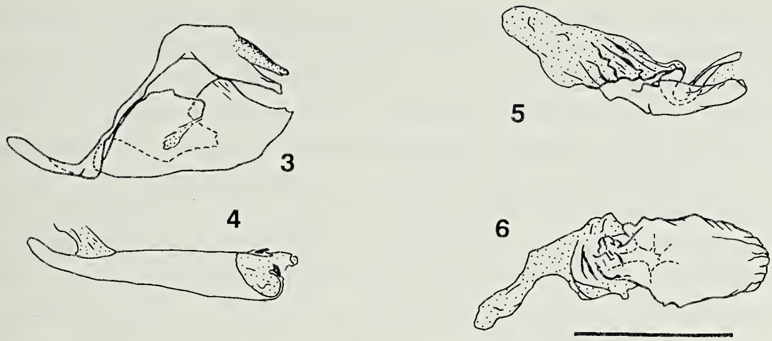
1. "smaller size" — Indeed, the type series is composed of specimens that are noticeably smaller than typical *E. dion*. However, all of the types were reared from a locality that also supports *E. dion*. Since reared specimens are often smaller than individuals that develop under natural conditions, it seems likely that the type series might have resulted from stressed larvae. I have produced similar-sized and patterned specimens (Fig. 2) from Ohio ova by providing larvae with very poor quality (low moisture content) cuttings of the sedge *Carex lacustris* Willd.

2. "more elongated fulvous streak throughout the cell in the ♂♂ on the secondaries" — The holotype male does not have a noticeably expanded streak on the hindwing. Furthermore, the expression of this pattern element is variable in the *E. dion/alabamae* complex, and the variation easily encompasses the pattern observed on the *E. macguirei* holotype.

3. "the absence of fulvous markings between the stigma and the base of the wings" — Again, this is a variably expressed pattern element in *E. dion*, and occasional specimens do not have any fulvous color between the stigma and the wing base (Fig. 7).

4. "the yellowish veins on the lower surface of the secondaries, which are absent or else poorly defined in [*E.*] *dion*" — The veins of fresh *E. dion* are always yellow and contrast strongly with the ground color. Freeman most likely compared reared *E. macguirei* with flown material of *E. dion*, and mistook the natural loss of scales from the veins of *E. dion* as a real pattern element.

5. "it differs" ... "in the genitalia" — Freeman's figure of the genitalia does differ significantly from any known *Euphyes*, and if it were accurate, might deserve generic status! However, the holotype



Figs. 3-6. *Euphyes macguirei* genitalia;
Fig. 3. male genitalia, lateral view; Fig. 4. aedeagus, lateral view; Fig. 5. female genitalia, lateral view; and Fig. 6. female genitalia, ventral view. Scale line = 2 mm.

Fig. 7. Phenotypic variation of wing pattern in Ohio and Indiana *E. dion*. These specimens were selected to show the range of variability. **First row,** left to right; OH., Logan Co., 16-VII-1983 (JS); OH., Williams Co., 18-VII-1954 (OSU); OH., Williams Co., 28-VI-1959 (OSU); IN., Steuben Co., 12-VII-1983 (JS); OH., Portage Co., 11-VII-1982 (JS). **Second row,** left to right; OH., Erie Co., VII-1896 (OSU); OH., Williams Co., 6-VII-1962 (OSU); OH., Logan Co., 16-VII-1983 (JS); OH., Williams Co., 16-VII-1955 (OSU); OH., Williams Co., 29-VI-1954 (OSU). JS = J. A. Shuey collection; OSU = Ohio State University Collection.

male possesses genitalia (Figs. 3 & 4) which do not differ in any obvious characteristics from the normal variation found in *E. dion* (Figs. 22-33), except that they are smaller. Likewise, the allotype female genitalia (Figs. 5 & 6) are very similar to variation within *E. dion* (Figs. 46-57).

Because every character which Freeman used to differentiate the taxon *E. macguirei* from *E. dion* is questionable, and because I can find no other characters which will separate these two taxa, I suggest that *E. macguirei* be considered a synonym of *E. dion* (Edwards). It is best to consider the type series of this taxon the result of unique rearing conditions.

Euphyes alabamae (Lindsey, 1923). Described from a single male as a race of *E. dion*, the status of this taxon also suffered from a lack of material. As late as 1931, Lindsey, Bell and Williams (1931) had collec-

tively examined only one additional specimen, a female. Clark and Clark (1951) elevated the taxon to specific status, commenting that it exists alongside normal *dion* in the Dahl Swamp of Virginia and that the orange pattern elements reliably separated these two species. They also noted that *E. alabamae* flies in late July, between the broods of *E. dion*. Klots (1951) considered *alabamae* to be a subspecies of *E. dion*, but noted that "a local colony of *A. d. alabamae* has been recorded from Dahl Swamp, Accomac[k] Co., Virginia; a most unusual record", thus, suggesting that these names may represent distinct species. Forbes (1960) accepted *E. alabamae* as a distinct species, reiterating the evidence presented by the Clarks. MacNeill (1975) was more cautious, relegating *alabamae* to a subspecies of *E. dion*, but noted that "a large geographical region of apparent overlap of these two subspecies suggests the need for much more information concerning their relationships." Miller and Brown (1981) re-elevated *E. alabamae* to specific status without comment. Most recently, Opler and Krizek (1984) considered the taxon to fall with in the normal variation of *E. dion*, citing personal communication with John Burns. John Burns (pers. comm.) has elaborated, stating that his position was not based on detailed investigation, but rather an inability to differentiate between these two taxa.

Indeed, when long series of southern "*E. alabamae*" are compared with series of northern *E. dion*, it is evident that wing pattern variation is rampant, and that there is no single character that will separate these supposed taxa. In my examination of long series of the *dion*/ *alabamae* complex from throughout eastern North America for wing pattern variability, three trends became obvious. First, northern populations are highly variable, and range from individuals that are bright orange (classic *dion*), to individuals that have greatly reduced orange pattern elements (classic "*alabamae*") (Fig. 7). These populations occur throughout glaciated North America, and extend south along the Atlantic Seaboard at least to Virginia. Second, populations from the Gulf Coast States are less variable, and have reduced orange pattern elements (Figs. 8 & 9). These populations match the concept of *E. dion alabamae*, as originally intended by Lindsey (1932). Finally, I describe as a new species one population from extreme southern Mississippi which has non-variable expanded orange pattern elements, and a narrow stigma (Figs. 8 & 9).

Furthermore, male and female genitalic comparisons between northern and southern populations failed to reveal any character that might be useful in separating these taxa. (In fact, all the species of the *dion* group are close [Shuey, 1986], and even easily recognized species such as *E. dukesi* are difficult to consistently separate from *E. dion* using genitalic characters alone [first noted by Lindsey, 1923].)

The original description of *alabamae* was, by necessity, typological. Because Lindsey was describing a single specimen, which obviously

differed from his concept of *dion* from northern states, no intrapopulational variability was considered. Once the concept of two distinct taxa separable by wing pattern became widespread (expanded orange = *E. dion*; reduced orange = *E. alabamae*), authors such as Clark and Clark (1951) and Forbes (1960) mistook variable populations as evidence for the sympatric occurrence of two distinct species. The material I have examined from the Dismal and Dahl Swamps of Virginia, do not substantiate any pattern of discrete broods between the two phenotypes. Because the *alabamae* phenotype can be found throughout North America and the only apparent difference between northern and southern populations is the reduction of phenotypic variability in the south, *alabamae* (Lindsey, 1923), should be relegated to a synonym of *E. dion* (Edwards).

A population from Bay St. Louis, Hancock County, Mississippi, differs from all known populations of *Euphyes*, and is here described as new.

Euphyes bayensis Shuey new species

Description. Male genitalia and female genitalia variable, placing the species within the *dion* group of *Euphyes*, but not different in detail from *E. dion*. Male stigma narrower ($\bar{x}=0.52\pm0.04$ mm) than in *E. dion* ($\bar{x}=0.79\pm0.09$ mm). Facies distinctive in several respects (Figs. 8-9); in both sexes, the orange and melanic colors are washed-out (paler) relative to *E. dion* (this difference is less noticeable ventrally); in males the forewing orange pattern elements are expanded and completely encircle the stigma (Fig. 8); female pattern variable, but always with conspicuous orange pattern elements on dorsal surfaces of both wings. Size; male forewing costa = 16.63 ± 0.48 mm; female forewing costa = 18.5 ± 0.53 mm.

Etymology. In the tradition of *Euphyes pilatka*, with which it flies, the name refers to the type locality.

Type Deposition. The entire type series was collected at Bay St. Louis, Hancock County, Mississippi by R. Kergosien. The holotype (19-IX-1970) and allotype (12-IX-1970) are deposited in the Carnegie Museum of Natural History. Paratypes are deposited as follows; three males (18-IX-1970, 10-IX-1970, 12-IX-1970), Carnegie Museum of Natural History; two males (9-IX-1970, 4-IX-1970) and one female (8-IX-1970), National Museum of Natural History; two males (21-IX-1970, 12-IX-1970) and one female (8-IX-1970), American Museum of Natural History; one male (17-IX-1970) and one female (18-IX-1970), Mississippi Entomology Museum at Mississippi State University; one male (10-IX-1970) and one female (18-IX-1970), Mississippi Natural Science Museum, Jackson; two males (both 19-IX-1970), The Florida State Museum at the University of Florida; one male (27-IX-1970), The Ohio State University; six males (two 19-IX-1970, two 10-IX-1970, 17-IX-1970, 19-IX-1970) and one female (18-IX-1970), J.A. Shuey collection;

and, 10 males (two 29-VIII-1970, 12-IX-1970, 17-IX-1970, three 18-IX-1970, two 19-IX-1970, 27-IX-1970) and three females (3-IX-1970, 21-IX-1970, 21-IX-1970), B. Mather collection. Three additional males (10-IX-1970, 17-IX-1970, 25-V-1971) in poor condition have been returned to B. Mather.

Discussion

My decision to describe *E. bayensis* as a new species is based on morphological and limited biological evidence and as such, is open to alternate interpretations. Although the male and female genitalia fall within the range of variation of *E. dion* (Figs. 10-57), wing pattern and stigma configuration differ consistently between *E. bayensis* and all *E. dion* populations (Fig. 8-9). Wing pattern differences include:

1. Color. The melanic ground color and the orange pattern elements are paler in both sexes of *E. bayensis* than in *E. dion* (Figs. 8 & 9). These differences are most noticeable above, and are less apparent ventrally. This color difference is real, and is not due to wear associated with flown specimens or fading of older specimens (all of the specimens figured were captured between 1970 and 1973).

2. Male pattern. Males of *E. bayensis* have consistently expanded orange pattern elements compared to males of *E. dion* from Mississippi. *Euphyes dion* males from the variable northern populations (Fig. 7) commonly approach the extent of orange pattern found, but southern populations of *E. dion* are less variable and are consistently dark. A graphic plot of one pattern element, the extent of orange along forewing vein V_2 (Fig. 58) reveals the trend towards the expansion of this element in *E. bayensis*.

3. Female pattern. Females of *E. bayensis* have consistently greater orange pattern elements than both northern and southern populations of *E. dion* (Figs. 8 & 9). The graphic plot of one pattern element, the extent of orange along forewing vein V_2 (Fig. 59), reveals that there is no overlap of variation between *E. bayensis* and Mississippi *E. dion*.

The most compelling morphological difference is the male stigma which is consistently narrower in *E. bayensis* than in populations of *E. dion* (Figs. 8 & 9). This relationship is demonstrated graphically in Figure 60. There is minimal overlap in stigma width between *E. bayensis* and *E. dion*.

Preliminary biological evidence for the specific differentiation of these taxa includes:

1. Habitat. The type series of *E. bayensis* was captured in a brackish marsh where it flies with *Euphyes pilatka*. *Euphyes dion* has never before been reported as a breeding resident in a brackish habitat (although the type locality of *E. alabamae*, Mobile Bay, is primarily a brackish complex) and normally occurs in fresh water wetlands; *E. dion* usually flies with *E. dukesi* in Mississippi (C. Bryson, pers. comm). Similar habitat differences separate other closely related pairs of

wetland butterflies and may be indicative of the speciation pattern of species that are restricted to these habitats (e.g., *E. dion* and *E. dukesi*; *Lyceana epixanthe* (Boisduval and LeConte) and *L. dorcas* Kirby; *Satyroides eurydice* Johannson and *S. appalachia* (Chermock); and *Poanes viator viator* (Edwards) and *P. viator zizaniae* Shapiro (see Shapiro, 1970; Shapiro and Cardé, 1970; Shuey, 1985).

2. Hostplant. The only known habitat is brackish, and dominated by sawgrass. Charles Bryson (pers. comm.) could not find *Carex hyalinolepis* Steud., the hostplant of *E. dion* in Mississippi, in the marsh. Thus it seems probable that *E. bayensis* does not use this *Carex* as the host.

3. Sympatry. Two specimens referable to *E. dion* (based on pattern) are known from the type locality (Fig. 61) and this species is generally distributed throughout Mississippi. The stigmas of these specimens are intermediate between *E. bayensis* and *E. dion* (Fig. 60). This evidence can be interpreted in two ways. I prefer to consider this as evidence of the sympatric distribution of closely related species. Supporting this position are; 1, the pattern and color of these two specimens which clearly places them as *E. dion*; and 2, the absence of intermediates between *E. bayensis* and *E. dion* from Bay St. Louis. However, the presence of these two males could also be interpreted as indicating that one species is represented at Bay St. Louis, and that intermediate phenotypes have simply not yet been collected.

Obviously, the biological evidence presented here needs to be confirmed, and additional populations of *E. bayensis* need to be located.

Acknowledgements. The entire type series of *E. bayensis* was brought to my attention by Bryant Mather, to whom I am deeply indebted. Other material was obtained from J.M. Burns (National Museum of Natural History); F.H. Rindge (American Museum of Natural History); M.D. Bowers (Museum of Comparative Zoology); J.E. Rawlins (Carnegie Museum of Natural History); J. Liebherr (Cornell University); C. Triplehorn (The Ohio State University); J.W. Peacock (Marion Ohio); and J.V. Calhoun (Westerville, Ohio). Charles Bryson (Stoneville, Mississippi) kindly permitted me access to copies of letters written by him to B. Mather. Roy Kendall (San Antonio, Texas) provided information about *E. macguirei*. Gordan R. Stairs and Richard L. Miller, The Ohio State University, provided access to laboratory space and photographic equipment respectively. John W. Peacock (Marion, Ohio), David C. Iftner (Worthington, Ohio), and Bryant Mather (Clinton, Mississippi) commented on earlier drafts. Finally, John M. Burns briefly examined part of the type series and, unknowingly, encouraged a lepidopterist who was otherwise discouraged about describing such a subtly differentiated taxon.

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Figs. 8 and 9. Phenotypic variation of wing pattern in *Euphyes bayensis* n. sp. and Mississippi *E. dion*.

Fig. 8. Dorsal wing pattern. **First Column**, *E. bayensis* n. sp., top to bottom (all Bay St. Louis, Mississippi.); Holotype male, 19-IX-1970; male, 17-IX-1970; male, 17-IX-1970; Allotype female, 12-IX-1970; female, 21-IX-1970. **Second column**, *E. bayensis* n. sp., top to bottom; male, 18-IX-1970; male, 19-IX-1970; male, 10-IX-1970; female, 3-IX-1970; female, 10-X-1970. **Third column**, *E. dion* top to bottom (all Mississippi); male, Lowndes Co., 26-VI-1973; male, Lee Co., 1-IX-1973; male, Lowndes Co., 8-IX-1973; female, Clay Co., 9-IX-1972; female, Lowndes Co., 10-IX-1972. **Fourth column**, *E. dion*, top to bottom; male, Clay Co., 13-IX-1972; male, Lowndes Co., 26-VI-1973; male, Lee Co., 8-IX-1973; female, Lowndes Co., 26-VI-1973; female, Lowndes Co., 9-IX-1973.

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Fig. 9. Ventral wing pattern. Legend as in Figure 8.

Fig. 61. *Euphyes dion* from Bay St. Louis, Mississippi. Left to right; 12-IX-1970; 2-IX-1970.

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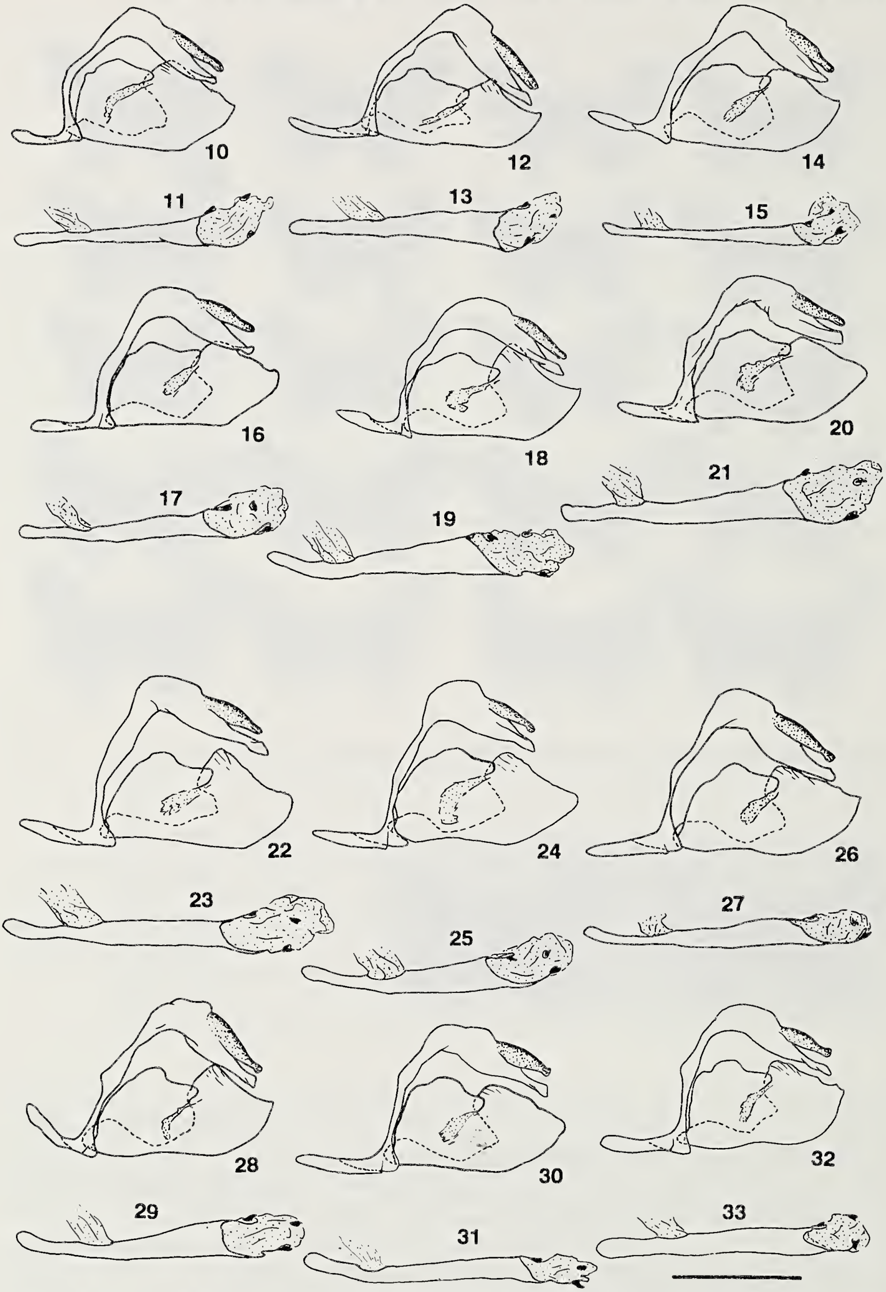
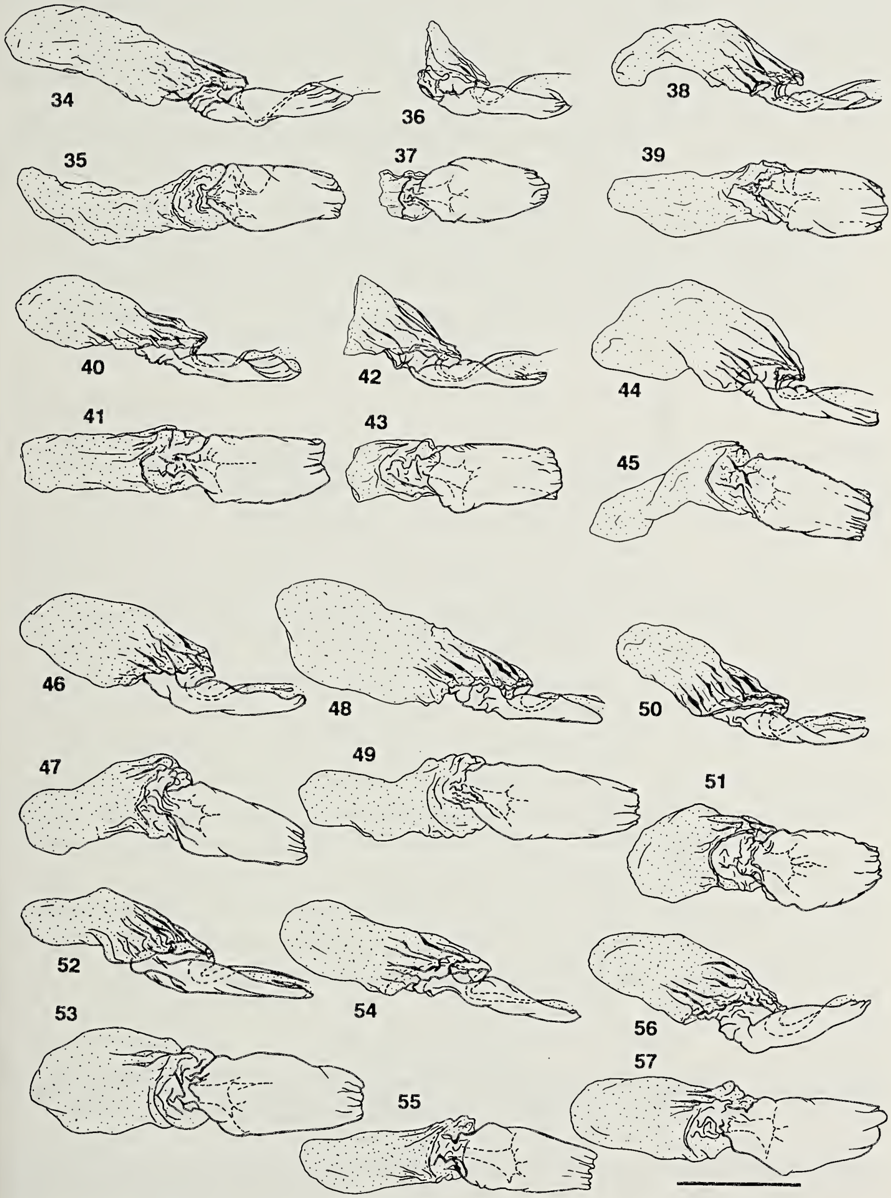
Figs. 10-33. The range of variation of male genitalia of *Euphyes bayensis* n. sp. and Mississippi *E. dion* (lateral view). Scale line = 2 mm.



Figs. 10-21. all *E. bayensis* n. sp., Bay St Louis, Mississippi; 10-11, 17-IX-1970; 12-13, 18-IX-1970; 14-15, 19-IX-1970; 16-17, 17-IX-1970; 18-19, 12-IX-1970; and 20-21, 21-IX-1970.

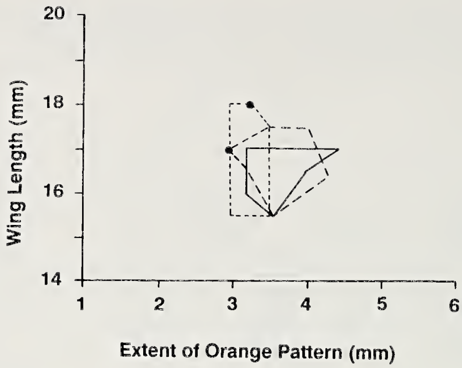
Figs. 22-33. all *E. dion*, Mississippi; 22-23, Lowndes Co., 26-VI-1973; 24-25, Lowndes Co., 8-IX-1973; 26-27, Lowndes Co., 3-IX-1973; 28-29, Lee Co., 1-IX-1973; 30-31, Lee Co., 1-IX-1973; and 32-33, Clay Co., 13-IX-1973.

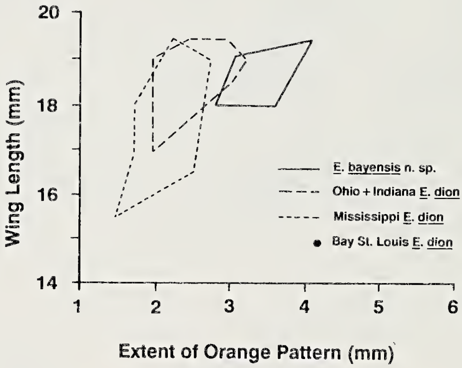
Figs. 34-57. The range of variation of female genitalis of *Euphyes bayensis* n. sp. and Mississippi *E. dion* (even numbers, lateral view; odd numbers, ventral view). Scale line = 2 mm.

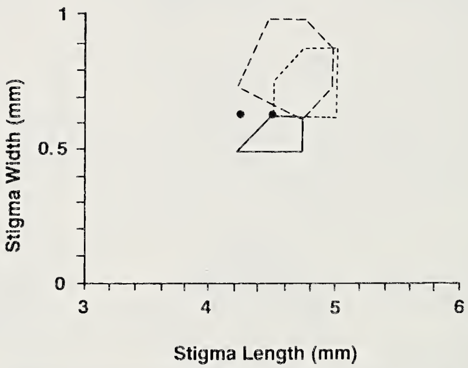


Figs. 34-45. All *E. bayensis* n. sp., Bay St. Louis, Mississippi; 34-35, 8-IX-1970; 36-37, 10-IX-1970; 38-39, 18-IX-1970; 40-41, 3-IX-1970; 42-43, 10-X-1970; and 44-45, 12-IX-1970.

Figs. 46-57. all *E. dion*, Mississippi; 46-47, Lowndes Co., 16-IX-1973; 48-49, Lowndes Co., 17-IX-1973; 50-51, Lowndes Co., 16-IX-1973; 52-53, Lowndes Co., 9-IX-1973; 54-55, Lowndes Co., 8-IX-1970; and 56-57, Clay Co., 9-IX-1972.







Figs. 58-60. Comparisons of pattern and stigma variation among *E. bayensis* n. sp., and Mississippi and Ohio + Indiana *E. dion*.

Fig. 58. Male forewing length versus extent of orange pattern along forewing V_2. Note the two specimens of *E. dion* from Bay St. Louis, which fall outside of the range of variation of *E. bayensis*, but within the range of variation of Mississippi *E. dion*.

Fig. 59. Female forewing length versus extent of orange pattern along forewing V_2.

Fig. 60. Stigma length versus width. Note that the two specimens of *E. dion* from Bay St. Louis fall between the ranges of variation for *E. bayensis* and Mississippi *E. dion*.

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The *Euphilotes battoides* complex: recognition of a species and description of a new subspecies. *(Lycaenidae)*

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Abstract. *Euphilotes bernardino* is recognized as a species separate from *E. battoides*, being cited here as a new combination. A discussion of the background for this action is given, in addition to that for describing a new subspecies, *E. bernandino garthi*, from the Isla de Cedros, Baja California.

Introduction

The paradox of Charles Darwin lay in the title of his immortal work. The crux of Darwin's thesis was that evolution proceeds from the natural selection of individual variants. Epling and Catlin (1950) were among the first to point out that the focus on "origin of species" was largely a result of Darwin's being forced to frame his arguments in taxonomic terminology because of the lack of any knowledge of genetics in his day. They went on to conclude that "Darwin should have emphasized his refutation of the fixity of species," because subsequent workers have unfortunately come to "regard the species not only as a taxonomic category but also as an evolutionary unit." Epling and Catlin conclude that the study of evolutionary processes can only be accomplished by testing individuals because there exist only two vehicles for adaptive change: individuals and breeding populations.

Yet taxonomy does have a vital role in permitting communication, as lucidly pointed out by Murphy and Ehrlich (1984). Biologists simply cannot work without "species," regardless of the merits of the method by which they are defined or other philosophic value they may have, real or imagined. Indeed, the Linnean nomenclatural system works with superb parsimony in providing an index of relationship whether based on phenetic, cladistic, or Gestalt methodology, I believe we all concur on the identity of the vast majority of "species," or clusters of similar appearance, by intuitive recognition of form (Gestalt), at least within the limited geographical areas with which we are familiar. Species identity has come to be "legitimized" by such elegant techniques as chromosome analysis, allozyme quantification, comparative biochemistry, statistical analysis of morphological characters, reproductive compatibility and so forth. A great deal of this work may represent what is a sort of fallacy of misplaced interpretation. Yes, these data do help circumscribe the "species;" and yes, these data are of indisputable

evolutionary significance; and yes, the cladistic concept is a valid approach to infer phylogeny; but no, this doesn't mean the species is a unit of evolution. Ehrlich and colleagues (Ehrlich and Raven, 1959 and Ehrlich and Holm 1962) discussed this subject matter in depth.

A closely related problem of taxonomy has arisen in regard to the utility of a taxonomic nomenclatorial approach to geographic variation within species. Since the landmark work of Wilson and Brown (1953), "subspecies," as the unit of geographic variation, has come to be viewed as arbitrary. The reasoned artificiality of subspecies is lack of concordance among multiple characters when these characters are quantified over the geographic range of variants. Gillam (1956) performed neat analyses of several well known polytypic butterfly species to verify the point. More recently, Hammond (1986) brought the arguments full circle in showing failure of concordance between both "species" and "subspecies" in *Speyeria*, he implies that neither category is more or less arbitrary than the other.

Thus, although taxonomic categories do not explain patterns of variation, categorization is useful for describing patterns of variation. With all organisms, application of names, at all levels, is a matter of responsibility, and will remain inherently controversial. Naming subspecies is no less valid than for any other category when reponsibly applied. As a matter of even greater issue today, in the United States, is that subspecies have assumed federal legal status under the Endangered Species Act. The Act provides protection to subspecies of threatened and endangered invertebrates, while uniquely variant populations of vertebrates can be listed. Conversely, a recent decision to not list the butterfly *Speyeria callippe callippe* (Boisduval) was based on the taxonomic assertion by Arnold (1985) that the variant populations proposed for listing did not constitute a valid subspecies. A more recent similar controversy did the result in the listing of *Euphydryas editha bayensis* Sternitzky.

Although arguments continue on both species and subspecies "problems," many represent a sort of continuing reinvention of the wheel. On balance there may be no more or less evolutionary information contained in any taxonomic category. Subspecies particularly serve to highlight patterns of variation which may be of special biological interest.

In the following I will perform some taxonomy, first to formally elevate a subspecies to the species level, because it makes rational sense. Second, I am naming a new subspecies of this species because it represents a large disjunction in appearance and is insular. In the process, the pattern of variation of these butterflies will be reviewed.

The species of *Euphilotes*

The genus *Euphilotes* (Mattoni, 1977) was named to circumscribe a group of five species. Later authors familiar with the group variously

recognized three (Shields, 1975, 1977), four (Miller and Brown 1981), or five species (Tilden and smith 1986). My present interpretation of the genus follows.

The species *E. enoptes* (Bdv.), *battoides*, (Behr), *rita* (B. & McD.), *pallescens* (Tilden & Downey, *and spaldingi* (B. & McD.) constitute five distinct morphospecies each clearly defined by several concordant characters of both male and genitalia and early stage morphology. The latter three species are allopatric, although *spaldingi* overlaps the other two in broad distribution. The three are clearly sister species, but should be regarded as distinct by virtue of several unique characters states. *E. mojave* should be rationally regarded as a species differentiated from *E. enoptes* by small but consistent differences in wing facies, female genitalia, and hostplant preference, in addition to sympatry (with and without synchrony) of several populations with other *enoptes* subspecies. Certain patterns of variation, distribution and natural history in the *E. battoides* set of entities imply a single species concept here cannot palpably describe the observed pattern of variation.

E. battoides is distinguished from its congeners at least by male and female genetalia, egg chorion morphology (Mattoni, unpubl.), fourth instar larva chaetotaxy and pattern (Ballmer and Pratt, 1988) and obligate univoltinism. As with all species of *Euphilotes*, populations are delimited by the spacial distribution and flowering times of their usually specific *Eriogonum* hostplants (see Shields, 1975). A number of subspecies have been described to reflect this variation. These are summarized as follows, with hostplant data from Shields (1975, 1977) and Pratt (unpubl.)

subspecies	distribution	flight time	*Eriogonum* hostplant
battoides (Behr)	Alpine Sierra, CA	July, Aug.	*lobbii, incanum, polypodum*
oregonensis (B. & McD.)	Casoades, OR	July	*marifolium, umbellatum*
intermedia (B. & McD.)	No. CA, So, OR	July	*marifolium, incanum*
glaucon (W.H. Edws)	E. CA, WA, OR, ID, MT, NV, B.C.	May-July	*umbellatum, heracloides flavum, sphaerocephalum*
comstocki (Shields)	Tehachapi Mts. CA	Aug	*umbellatum*
centralis (B. & McD.)	CO, UT, NM, AZ	July-Aug	*umbellatum, jamesi corymbosum*
baueri (Shields)	CA, NV	May	*ovaliforlium, kennedyi*
bernandinio (B & McD)	S & Cent CA, Baja CA	Apr-July	*fasciculatum, cinereum*
martini (Mattoni)	Mojave; CA, AZ	Apr-May	*fasciculatum*
allyni (Shields)	El Seg. Dunes, CA	July-Aug	*parvifolium*
garthi (new)	Cedros Island, Baja CA	Mar-June	*fasciculatum*
ellisi (Shields)	E. CA, NV, AZ, CO, UT	July-Sept	*corymbosum, heermannii, microthecum heermannii*

The relationships among the above taxa are more complex than given and may be more accurately dealt with as several species. The model of one monophyletic grouping exhibiting simple geographio polytypy does not square with the data: e.g. sympatry and synchrony of *battoides* and *intermedia* at Gold Lake, CA, sympatry and allochrony of *glaucon* and *baueri* at Westgard Pass, CA; sympatry and allochrony of *martini* and

ellisi in several mojave desert range; sympatry and allochrony of *ellisi* and an undescribed taxon in northern Arizona, and the parapatry (sympatry?) and synchrony of *glaucon* and *bernardino* at several sites along the east slope of the southern Sierra Mevada. As an initial step in attempting to more clearly reflect the pattern of variation in the group, I propose the following concept:

Euphilotes bernardino (Barnes & McDonnough 1917) new combination

The species includes the cluster of four closely related taxa commonly recognized as subspecies of *battoides*: *bernardino* (B. & B. 1917), *martini* (Mattoni, 1954), *allyni* (Shields, 1975), and *garthi* (new spp.). Synapomorphic characters of the species include: 1) exclusive hostplants *Eriogonum fasciculatum, E. cinerium,* and *E. parvofolium* 2) small mean adult size (wingspan <11.0 mm) and 3) fourth instar larva morphology and pattern (Pratt, unpub.). The suite of variable wing pattern characters which discriminate the four subspecies is given in Table 1.

Although recognition of *E. bernardino* as a "species" is based on weak wing characters, size and larval hostplant, and larval characters which may not stand up to scrutiny of the many populations not surveyed, the sympatric criterion is consistent. Future work may well discriminate other species in the remaining "*battoides*" group. The taxon *glaucon*, for example, passes the sympatry test in some localities has a large geographic distribution, shows extensive wing pattern variation, and uses several foodplants. Complete information on *glaucon* over its range and in relation to its nearest nieghhors is not sufficient to override the consideration of conservatism.

Classification of the populations of *E. bernardino*

INTRAPOPULATION VARIATION AND WING PATTERN TERMINOLOGY

The degree of variation in wing pattern elements in adult *Euphilotes* is shown in Figure 1. Pairs of specimens were selected from five series of both *E. enoptes* and *E. battoides* to show extremes of both upper and underside variation in both sexes. Such extremes are frequent when dealing with series and underline the care that should be taken in arriving at taxonomic descision in the group of butterflies.

The description of wing characters in polyommatine blues has been very inconsistent in the past for lack of a standardized nomenclature to apply to the various elements of pattern which repeat through the group. Nabokov (1943) attempted to rectify the matter by suggesting a detailed terminology. I have in large part followed his system, which is graphically presented as figure 2. Interspaces are designated by the named vein anterior to the space. The lower part of figure 2 diagrammatically classifies fringe types which are found throughout the tribe

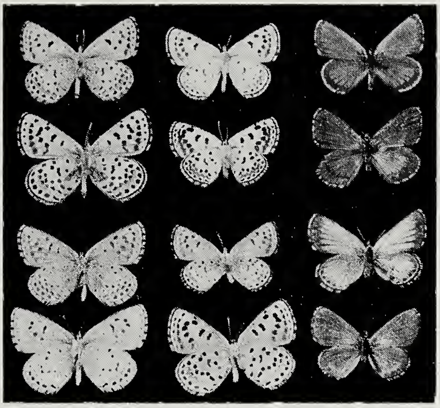


Fig. 1. Intrapopulation variation exhibited by selected pairs of *Euphilotes*. **Top two rows**, left to right. *E. enoptes ancilla*, ♀ UNS. Montana, 9 mile canyon, 20 vi 82. S. Kohler. *E. pallescens pallescens*. ♀ UNS. Nevada, Lincoln Co. 2 mi NE Hancock Summit, 24 viii 78, O. Shields. *E. battoides centralis*, ♂ UPS. Colorado, Chaffee Co. O'Haver Lake, 30 vi 68, R. Mattoni.
Bottom two rows. *E. Battoides intermedia*, ♂ UNS, California, Siskiyou Co. Castle Lake, 21 vii 77, T. Dimock. *E. battoides ellisi*, ♀ UNS. Arizona, Coconino Co. 9 mi. E. Winona, 20 viii 79, R. & L. Mattoni. *E. battoides baueri*, ♀ UPS. California, Inyo Co. White Mt. Rd. 2. mi. N. Hwy. 168. 5 vi 76, R. & N. Mattoni.

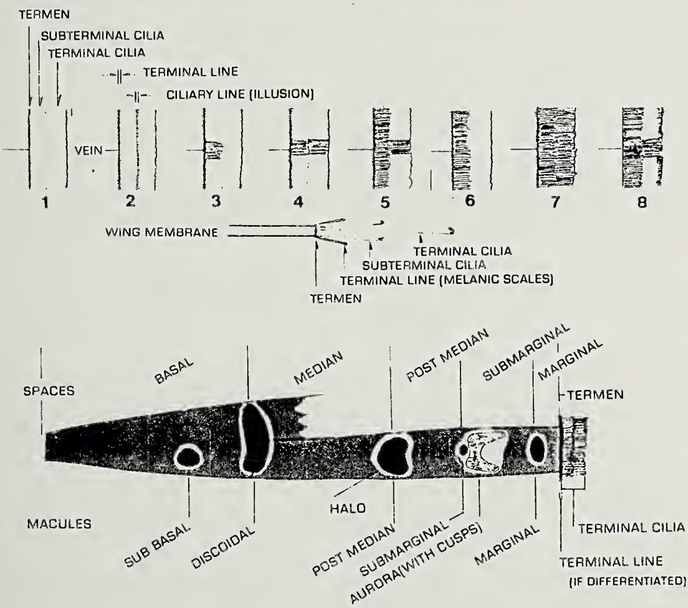


Fig. 2. **Upper.** Nomenclature for wing pattern elements in *Euphilotes* (and most Polyommatine blues). Diagrammatic representation of UNH macules and marks across M_1 (cut-away) and M_2. Interspaces named for anterior vein.
Lower. Fringe types as character states at CU_1.

Table 1. Comparative data of samples of populations of *Euphilotes battoides: garthi* (type series, data in text), *allyni* (ES = CA, Los Angeles Co., El Segundo Dunes, Chevron Refinery, 25 VII 65, Mattoni, leg.), *allyni* (PV = CA. Los Angeles Co., Palos Verdes Peninsula, Crenshaw, 27 VII 83, Mattoni, leg.), *bernardino* (CA, Los Angeles Co., Santa Monica Mts., Mulholland Dr. & Sepulveda, various dates, Mattoni, leg.), *martini* (AZ, Yavapai Co. I-17 at Bumblebee cutoff, 17 IV 79, Mattoni, leg.). *f.* = Frequency. Boldface numbers indicate character state sets unique to that subspecies. Refer to Fig. 2 for numeration.

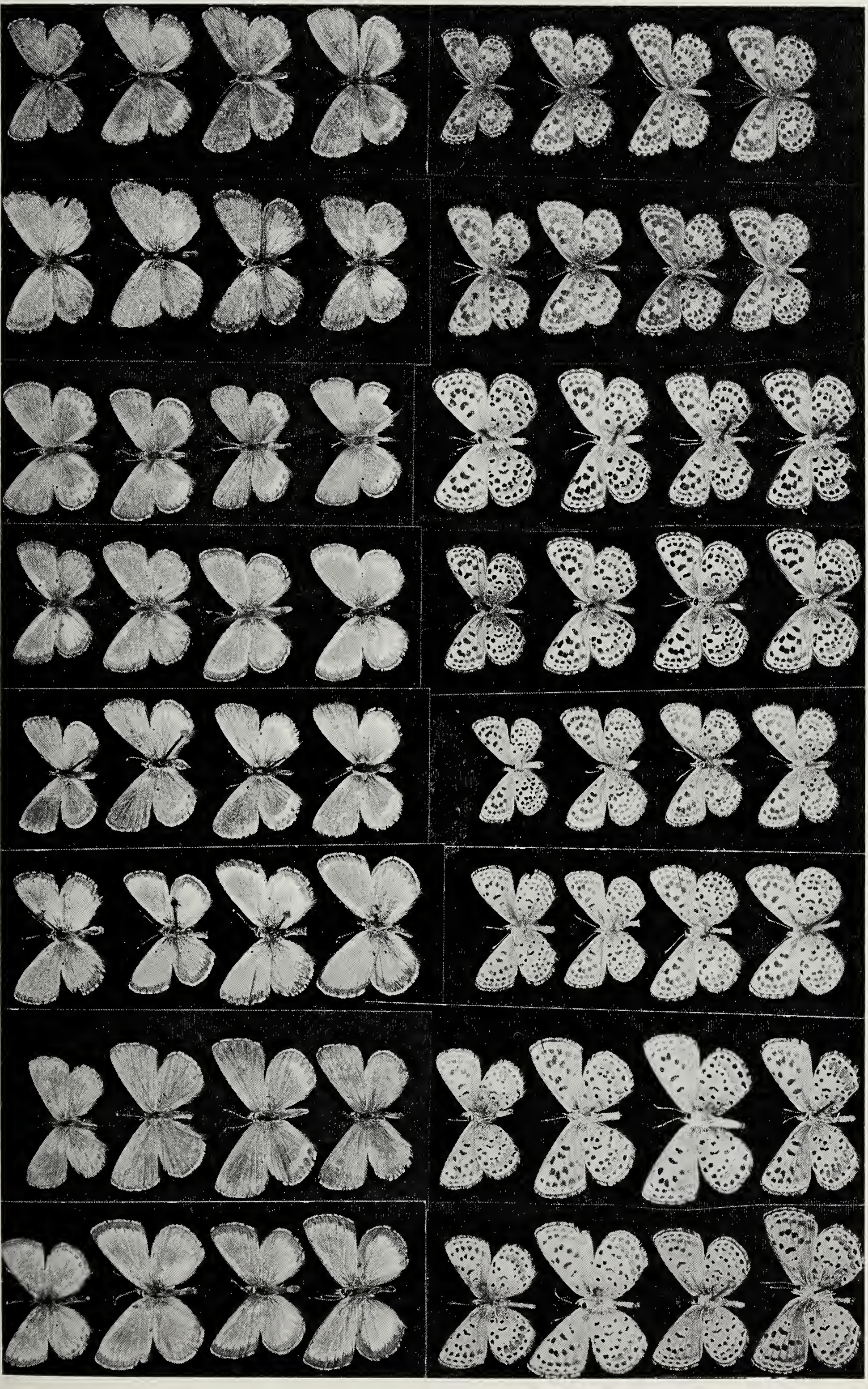
		garthi	*allyni*		*bernardino*	*martini*
			ES	PV		
Wingspread-mm						
Males	Mean	10.1	10.3	10.8	10.0	10.9
	Range	8.7-10.9	9.4-11.0	10.0-11.5	9.3-10.5	10.0-12.3
	N	11	10	10	7	11
Females	Mean	9.9	10.0	10.3	9.5	10.7
	Range	9.4-10.4	9.4-10.5	9.8-10.9	8.5-10.2	9.9-12.0
	N	5	10	10	8	10
Males-Upperside						
FW-Marginal Bandwidth-mm		**1.26**	**1.10**	**1.01**	**0.59**	**0.86**
HW-f. with aurora		1.0	0.8	0.9	0.1	0.3
f. with checkered fringe M_3		1.0	0	0	0	0.7
Underside						
f. with halos		0	0	0	0	**0.8**
FW-width PM macule mm M		**1.20**	**0.99**	**1.00**	**0.80**	**0.70**
f. dissociated PM macs.		**0**	0.6	0.9	0.7	**1.0**
f. without marg. mac. R_{4+r}		0.5	0.9	**0.4**	0.3	0.5
f. Cu_2 Suffusion		0.5	0	0.1	0	0.6
HW-f. dissociated aurora		1.0	10	1.0	0.7	**0.2**
f. fringe type 4		**0.7**	0	0.1	0	0
Females-Upperside						
HW-width aurora M_3 mm		0.88	**1.59**	**1.87**	1.50	0.96
f. distinct marg. macs.		0.2	1.0	1.0	1.0	0.8
Underside						
f. with halos		0	0	0	0	**0.5**
FW-width PM mac. mm M		**1.43**	**1.09**	**1.13**	0.93	0.85
f. with aurora		**0.2**	0.9	0.8	0.5	0.6
f. dissociated PM macs.		**0**	0.2	0.3	0.4	**1.0**
f. without marg. mac. R_{4+5}		1.0	0.6	0.1	0.5	0.4
f. Cu_2 Suffusion		0.6	0.7	0.7	**0**	0.4
HW-f. dissociated aurora		1.0	1.0	1.0	0.7	**0.2**
f. fringe type 4		**0.8**	0.1	0.1	0	0
Foodplant		fasciculatum	parvifolium	cinereum	fasciculatum	fasciculatum

Notes

1. *allyni* ♂ homoeotic DV transposition of cyanic scales over distal part of Cu_2-UNF.
2. *martini* dimorphic for an elongated tear shaped posterio-distal pointed UNF PM macule in M_2 in .3 males and .8 females and subsequently noted in other population of *martini*.

and are useful characters. The cross section of the termen illustrates how the illusion of various fringe patterns is produced. The set of character states used in this study are given in Table 1.

Fig. 3. Subspecies of *Euphilotes bernardino*. UPS, 4 specimens above, UNS the same 4 specimens below. About 0.9 life size.
Rows 1 and 2, ♂ and ♀ *E. b. martini*, Arizona, Yavapai Co. Bumblebee turnoff of 1–17, 17 iv 79 R. Mattoni.
Rows 3 and 4, ♂ and ♀ *E. b. bernardino*. California, Los Angeles Co. Mulholland Hwy. various dates, May, R. Mattoni.
Rows 5 and 6, ♂ and ♀ *E. b. allyni*, California, Los Angeles Co. Chevron plant, El Segundo, 25 vii 65. R. Mattoni.
Rows 7 and 8, ♂ and ♀ *E. b. garthi* from type series: see data in text.



Relationship of subspecies

There are 4 subspecies of *E, bernardino* (Table 1). Of these, one has not been formally described, although recognized for some time (Rindge, 1948):

Euphilotes bernardino garthi Mattoni *new subspecies*

Males. Fig. 3. Table 1. Distinguishable in every specimen available from all other subspecies by 1) UPF marginal bandwidth, 2) UPH marginal band not dissociated, 3) UNS macules, particularly the post median (PM) set, extremely large, PM set arranged without dissociation between interspaces, 4) UNH fringe type 4.

Females. Fig. 3. Table 1. Distinguishable in all specimens by 1) UPH aurora not extending distally to wing margin such that marginal macules are not differentiated, 2) underside characters as in males.

Genitalia. Indistinguishable in either sex from any member of the *E. battoides* complex.

Type material. Holotype male, Baja California Norte, Isla de Cedros, canyons west of Punta Norte, 1 IV 1983 (Faulkner and Brown). Paratypes some locality as holotype, dates as follows: 2 ♂♂ 30/III, 4 ♂♂ 4 ♀♀ 1/IV, 1 ♂ 2/IV, 1 ♂ 1 ♀ 1/VII, 2 ♂♂ 3/VII, all 1983 all leg. Faulkner and Brown. 3 ♂♂ "Mexico, Cedros Island, 15/III/39" no. leg cited (presumably F. Rindge) colln. LACMNH. **Disposition of types**. Holotype, 5 male paratypes and 4 female paratypes deposited in the SDNHM; 1 male and 1 female paratype deposited in CAS, San Francisco; 3 male and 1 female paratypes despoited in the LACMNH; 1 male and 1 female paratype deposited in the Instituto de Biologia, National University of Mexico, Mexico City; 1 male and 1 female deposited in the USNM, Washington.

Distribution. *E. bernardino garthi* is an apparent disjunct population of the species endemic to Cedros Island. Although the indicated larval hostplant occurs throughhout the island, the insect was only found in March and April at low elevations in the washes and canyons of the north end of the island, and at higher elevations in July.

Natural History. The larval hostplant in all likelihood is *Eriogonum fasciculatum* Bentham with which the adults were exclusively associated. The insect also appears univoltine, with an extended emergence taking place as the season extends altitudinally. This pattern corresponds to the development of foodplant flowering which is essentil for adult nectaring, oviposition, and larval growth. A report of Faulkner and Brown discusses Cedros Island and its butterfly fauna in detail.

Etymology. The subspecies nomen is a patronym honoring Dr. John Garth for his early work on the biology of Baja California and especially Isla de Cedros.

Discussion

E. bernardino garthi is an endemic of Isla de Cedros, where it probably evolved in isolation since the eustatic sea level rise after the last glaciation. Indications of evolutionary history might be inferred from study of any *E. bernardino* populations their foodplants on the adjacent mainland, Natividad island which was also connected to the mainland, and San Benito island which is oceanic. Simultaneously, insight might be shed on the emigration potential of *Euphilotes*, which is unknown from all the Channel Islands (Miller, 1985), although Santa Rosa and Catalina islands have populations of proper foodplants.

Quantitative data on wing characters, determined to the be variable over the whole array of *Euphilotes* species, are given for the four subspecies of *E. bernardino* in Table 1. Certain character states can be used to classify all specimens of the species almost unequivocally into an appropriate subspecies following Table 1. The single character state which may serve to identify each taxon is the relative amount of melanin in the underside macules. The character is expressed by the width of the PM macule of forewing M_3 in in table 1. I illustrate the character in a short series of specimens of each taxon in figure 3, which also provides information on variability in wing pattern as well as other characters. The cline of increasing darkening exhibited by each subspecies from the desert to coastal environments is concordant with two additional characters of the males: 1) upperside cyanic overlay and 2) marginal band width. It must be emphasized that these clines are sharp step clines, with the steps corresponding to the subspecies limits. *E. bernardino bernardino* populations on the desert edges of the San Bernardino and San Jacinto mountains appear somewhat lighter than cis-montane populations, but these are not clinal in other traits which might confuse them with *martini*, Scoring individuals from *bernardino* colonies at Lytle Creek (south side of the San Gabriel mountains) and Horsethief Canyon (north side of the San Bernardino range) showed them to be statistically identical in character states to the data given in Table 1.

The two darkest subspecies, *garthi* and *allyni*, are associated with hot daytime weather during their flight times, with most moisture coming from frequent dense fogs and not rainfall. The two no doubt evolved independently under what may be similar environmental conditions, the intervening 700 km are occupied by populations of *bernardino*.

The distribution of the four subspecies is shown in figure 4. The data are largely from Shields (1977) plus a few newer records. The occurrence of *bernardino* is probably almost continuous, corresponding with the continuous distribution of its hostplant *Eriogonum fesciculatum* across most of southern California. However, following the coast ranges north of Santa Barbara the hostplant becomes increasingly disjunct. The

subspecies *martini* is completely disjunct, nowhere directly meeting *bernardino*. Through the desert mountains of eastern California, southern Nevada, and western Arizona, martini occurs as a series of isolated colonies. From central Arizona east it is more continuous as it occurs over the belt of *Eriogonum fasciculatum* which grows in a band along the south slope of the Mogollon Plateau and then ranging into southern Arizona and probably Sonora.

The precise distributional boundaries of *bernardino* are not defined where it ranges into west central Nevada. The two populations in fig. 4 were cited by Shields (1977) from Churchill Co., who made the specimens available. Although highly suggestive of *bernardino*, they must remain unassigned until further collections are available. The populations were associated with *Eriogonum heermanii* and Austin (pers comm.) found similar populations, also on *E. heermanii*, in the southern Toiyabe mountains. These represent the first documentation of *Euphilotes bernardino* on *Eriogonum heermanii*.

Across the area which would provide any contact zone between *Euphilotes bernardino bernardino* and *E. b. martini*, populations are found as isolates in desert mountain "islands." There are no data, other than anecdotal, to indicate the two "blend" in any manner as suggested by both Langston (1969) and Shields (1977). The Beatty, Nye County (Shields, 1977) specimens were scored and completely overlap the data given in Table 1, including dimorphism for the same peculiar PM macule as cited. The *martini* population of the Providence Mountains was also identical by the same criteria. The term "blend" is a very unfortunate term which has found its way into wide use in the literature. By implication "blend" is usually taken to mean the result of gene flow causing blending of character states. However, in all but the most rigorously tested cases, it is not possible to discriminate between hybridization or introgression and adaptive selection along an environmental gradient (Endler, 1977), but see Collins (1984) for a well documented study in the Lepidoptera.

The fine grain distribution of the *bernardino* and *allyni* interface is well established, although precise classification of the interface population (s) is open to interpretation. *E. bernardino allyni* occurs only on the historic El Segundo sand dunes, which comprised four distinct segments prior to the urbanized destruction of southern California. It is extinct on two segments (Mattoni, 1989). It is solely restricted to *Eriogonum parvifolium* as larval hostplant, although females will oviposit on both *E. cinereum* and *fasciculatum* in field and choice experiments. Mattoni (unpub.) has evidence that the latter two species are toxic to neonate larvae from El Segundo Dunes stock. Today *Euphilotes bernardino allyni* is known from only three sites: 1) the 1 Ha type locality at the Chevron refinery preserve, 2) on about 10 Ha at the Los Angeles International Airport (LAX) dunes property and 3) on a <0.5 Ha site at Malaga cove. The latter, at the northwest base of the Palos Verdes

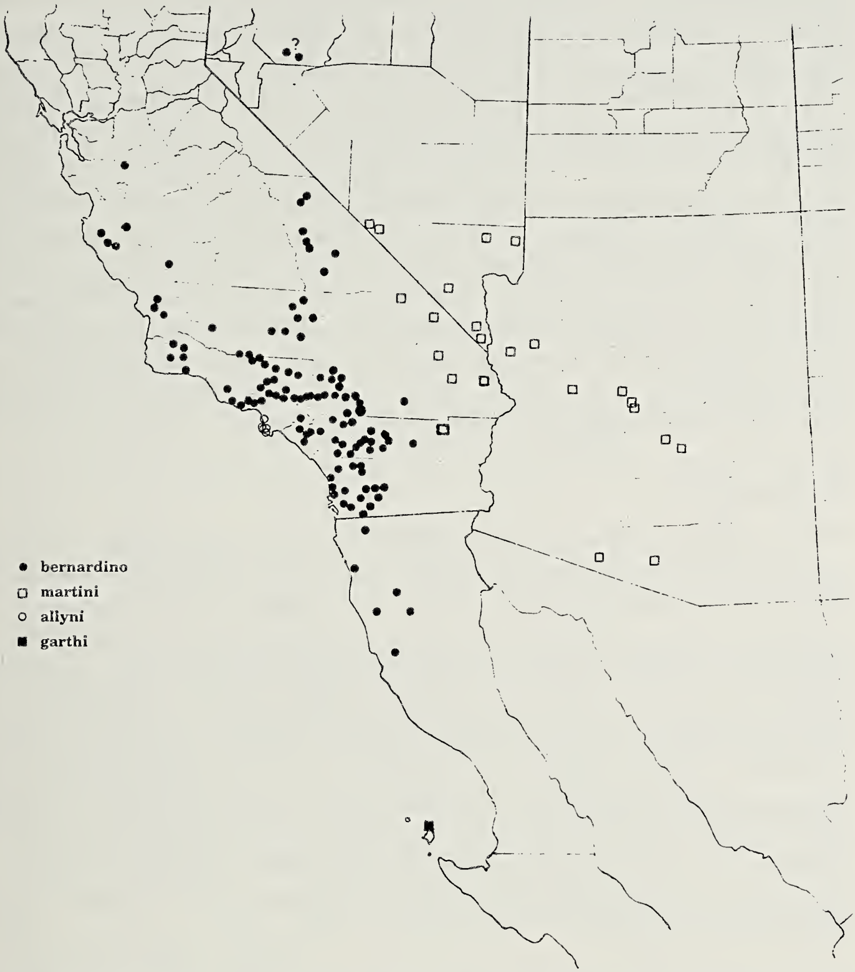


Fig. 4. Distribution map of E. bernardino and its subspecies discussed in text

peninsula, is isolated by one kilometer from the south where the buckwheat *Eriogonum cinereum* becomes common, growing intermixed with *E. parvifolium* along the seacliff. At this point there is a shift in butterfly ecotype to a taxon which is best referred to *bernardino* on the basis of natural history, although phenetically it overlaps the wing pattern of *allyni*. At the higher elevations on Palos Verdes, the host-plant occurs as pure stands of *E. cinereum*, but also includes a few colonies of *E. fasciculatum* which grown in the canyons of the north slope. It is not known if the butterfly feeds on the latter plant.

Examination of the topographic survey maps, and aerial and other photographs taken prior to significant urbanization in the 1930's showed that the scrub communities of both the El Segundo Dunes and

the Palos Verdes penisula were surrounded and isolated by low forb meadows. Further, the penisula was isolated from the major dunes site. The latter is reflected in two butterfly distributions: the now extinct Palos Verdes Blue, *Glaucopsyche lygdamus palosverdesensis* Perkins and Emmel, which evolved independently from *G.l. australis* Grinnell, a still abundent species on the dunes; and the occurrence of an *Apodemia mormo virgulti* (Behr) ecotype on the dunes which is absent from Palos Verdes. These findings indicate that the *Euphilotes bernardino bernardino* populations found today at Palos Verdes are relicts from some time since the last glaciation when a continuous belt of *Eriogonum fasciculatum* must have connected to th coastal sage communities to the north. *Euphilotes bernardino allyni* on the other hand must have evolved in situ and in isolation during the formation of the El Segundo sand dunes over the past 4–6000 years.

Conclusions

The nature, meaning and proper use of species and subspecies concepts will no doubt remain an idle and infinite speculative endeavor. However, for the purposes of the above description of patterns of variation of the *bernardino* part of the *E. battoides* complex, the general application of kind (species) and reasonably concordant geographically distributed kind (subspecies) suffices. There is no evolutionary connotation inherent in either category itself, although two modal sorts of subspecies variant classes are included: *bernardino* and *martini* with large geographic distributions and inclusion of many probable ecotypic clusters (genetically differentiated populations adapted to local environmental conditions) , and *allyni* and *garthi* which are highly restricted endemic populations each of which may be, or recently were, essentially panmictic.

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Note added in proof: A recent paper by O. Shields and J. Reveal (1988. Sequential evolution of *Euphilotes* (Lycaenidae, Scolitantidini) on their plant host *Eriogonum* (Polygonaceae; Eriogonoideae). J. Linn. Soc. 33:51–91) was received after this paper was in final proof. Shields proposed therein to elevate *bernardino* to species status, an action supported by the above, with the exception of *E. battoides ellisi*. This combination is illogical because of sympatry (but allochrony) with *E. bernardino martini*. Consideration of *ellisi* as a subspecies of *bernardino* is insupportable because of chaetotaxy (Pratt, unpublished), foodplant, adult pattern and size, and seasonal adaptedness. These characters firmly place it in the *battoides* group.

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Genetic experiments with a *calverleyi*-like mutation isolated from *Papilio bairdi oregonius* (Papilionidae)

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Abstract. A major aberration in the wing pattern of the black *Papilio polyxenes asterius* was discovered and named *calverleyi* in 1864. Recently a similar mutation was isolated in the yellow *P. bairdi oregonius*. Genetic experiments suggest that this trait is inherited as a simple Mendelian recessive, although possible deleterious effects from this trait may increase mortality rates among the homozygotes in certain family lines. In order to compare the *oregonius* mutation with the original *calverleyi* phenotype, it was necessary to combine the *oregonius* gene with the black wing pattern. This was accomplished by hybridizing the *oregonius* stock carrying the gene with black forms of *P. bairdi, P. polyxenes asterius*, and *P. joanae*, and successfully producing a phenotype nearly identical to the original *calverleyi* aberration.

Introduction

The *Papilio machaon* complex is represented in North America by many differentiated populations that have been traditionally regarded as distinct taxonomic species (Howe, 1975; Tyler, 1975). However, *P. indra* Reakirt is the only member of this group that is particularly distinct in morphology, including larval color pattern, pupal morphology, and adult male genitalic structure. In addition, artificial hybrids produced by crossing *P. indra* with other members of the *machaon* complex are apparently not viable, and did not survive beyond the first larval instar in one experiment (Emmel & Emmel, 1964).

All other taxa within the *machaon* complex are partially or completely inter-fertile (Clarke & Sheppard, 1955), and can be hybridized and back-crossed for various genetic experiments of the type reported in the present paper. Mating crosses are accomplished using the hand-pairing technique described by Clarke (1952).

Nevertheless, three or four groups of populations may be recognized as distinct biological species based upon reproductive isolation and

ecological segregation in zones of sympatry. These are outlined as follows.

1. *Papilio machaon* Linnaeus. This Eurasian species also includes two subspecies distributed in the arctic and alpine regions of Alaska and Canada. However, Sperling (1987) has recently documented extensive hybrid swarms between one of the subspecies and several members of the *P. polyxenes* group in central Canada. This suggests that these groups may be regarded as conspecific, despite the divergence in wing color pattern and allozyme patterns observed by Sperling (1987). Larval foodplants are *Artemisia arctica* Less and Umbelliferae (Tyler, 1975). *P. machaon* populations are monomorphic for the yellow color form of the adult except in hybrid suture zones.

2. *Papilio polyxenes* Fabricius. This group consists of at least seven well-differentiated subspecies or semispecies that are allopatric throughout much of North America, extending from Newfoundland to British Columbia and southward to Cuba and the Andes of South America. Larval foodplants are Umbelliferae and Rutaceae. The group is polymorphic with both yellow and black color forms in the adult, but the subspecies *asterius* Stoll used in the present experiments is monomorphic for the black form.

3. *Papilio bairdi* Edwards. This group includes four or five subspecies that are widely distributed in the arid regions of western North America, and are sympatric with members of the *polyxenes* group throughout their distribution. *Artemisia dracunculus* L. is apparently the only larval foodplant. As with the previous group, *P. bairdi* populations are polymorphic in adult color. Of those used in the present experiments, the typical subspecies consists primarily of the black form, while the subspecies *oregonius* Edwards is monomorphic for the yellow form.

4. *Papilio joanae* Heitzman. This is a local endemic restricted to central Missouri. It is weakly differentiated from *P. polyxenes asterius*, but does exhibit both reproductive isolation and ecological segregation from sympatric populations of this latter species (Heitzman, 1973). Larval foodplants of *P. joanae* are restricted to certain Umbelliferae. The species is monomorphic for the black form.

A very colorful aberration in the wing pattern of *P. polyxenes asterius* was named *calverleyi* by Grote (1864), and was illustrated in a color plate. In this variant, the black submarginal borders normally found in swallowtails of the *machaon* complex are completely absent on both the fore and hindwings, so that the yellow median area of the wings extends to and fuses with the yellow submarginal spots.

The original specimen was a male captured August, 1863 on Long Island, Queens Co., New York. A female of similar aberration type was subsequently captured in April, 1869 near Enterprise, Florida (Mead, 1869). Both specimens were illustrated in color by Edwards (1884), and the female was also illustrated by Holland (1899).

Fig. 1. Top row (left) normal *oregonius* male, (middle) "cal" *oregonius* male, (right) "cal" *oregonius* female with extensive orange. Middle row (left) normal *oregonius* female, (middle) "cal" *oregonius* female, (right) normal H3 *joanae* hybrid female (Jo-Or-Bd-TC 86-1). Bottom row (left) normal H3 *asterius* hybrid male (As-Or-Bd-TC 86-1), (middle) "cal" H3 *asterius* hybrid male (As-Or-Bd-TC 86-2), (right) "cal" H3 *joanae* hybrid female (Jo-Or-Bd-TC 86-1) with extensive orange.

On July 13, 1984, D. V. McCorkle captured a near-normal female of *P. bairdi oregonius* along the Columbia River at Celilo in Wasco Co., Oregon. The specimen displayed an unusually large amount of orange in the median area of the ventral hindwing. From the progeny of this female, a brother-sister mating (Or 84-1 F-2) was performed in an attempt to intensify the orange coloration through inbreeding. Of approximately 40 progeny produced from the sibling mating, 33 specimens were of a normal phenotype and 7 specimens were of a *calverleyi*-like phenotype (abbreviated "cal") in which the black wing borders were completely absent (fig. 1). As a consequence, the normal black and blue coloration of the wing borders is replaced by yellow and orange pigmentation. The numbers of the "cal" and normal phenotypes are not significantly different from the 3:1 ratio that we would expect by simple recessive inheritance for this mutation ($\chi^2 p < .28$). Because both of the sibling parents must have been heterozygote carriers of the trait to produce this ratio, the mutation must also have been carried by one of

Table 1. Experimental crosses used in the production of "cal" phenotypes.

Generation	Mating No.	Parentage male × female	Phenotypes normal	Phenotypes "cal"
F2	Or 84-1 F-2	Celilo oregonius (sibling cross)	33	7
H1	Or-Bd 85-6	bairdi × Celilo oregonius (Or 84-1 F-2)	59	0
H2	As-Or-Bd 86-3	Or-Bd 85-6 × asterius	20	0
H2	Jo-Or-Bd 86-1	Or-Bd 85-6 × joanae	10	0
H3	As-Or-Bd-TC 86-1	As-Or-Bd 86-3 × Celilo oregonius (Or 86-1)	46	3
H3	As-Or-Bd-TC 86-2	Celilo oregonius (Or 86-3 F-2) × As-Or-Bd 86-3	4	1
H3	Jo-Or-Bd-TC 86-1	Jo-Or-Bd 86-1 × Celilo oregonius (Or 86-1)	38	7

the original wild parents at Celilo, either the male or the female. Although several other wild butterflies from Celilo were tested for this trait by inbreeding, the "cal" phenotype did not appear in other family lines.

Since the "cal" specimens displayed the same extensive orange coloration on the hindwings as their normal parents and wild grandparent, it was thought that this trait might be linked with the "cal" mutation, and would thus serve to identify heterozygote carriers of "cal". Unfortunately, subsequent crosses decoupled the orange coloration from the "cal" phenotype, proving that these traits are independently inherited (fig. 1).

Of course, the basic color background for the above "cal" mutation is of the yellow *oregonius* form, rather than the black *asterius* form of the original *calverleyi* specimens. For those readers unfamiliar with the genetics of the *Papilio machaon* complex, the black form is a simple Mendelian dominant over the yellow form (Clarke & Sheppard, 1955). Thus, we decided to test the hypothesis that the *oregonius* "cal" mutation is similar to or identical with the original *calverleyi* aberration in *asterius*. This was accomplished by combining the *oregonius* "cal" mutation through hybridization with the black form, and producing a black *calverleyi*-like phenotype very similar to that of the original specimens obtained by Grote and Mead in the 19th century (fig.

1). It should be noted that the original Mead female is of the early spring form with a well developed yellow median band and discal bar. By contrast, our specimens are of the summer form in which these yellow markings are mostly absent in black females.

As shown in Table 1, we crossed our Celilo *oregonius* stock carrying the "cal" trait with a black *P. bairdi bairdi* Edwards stock that was originally obtained from near Flagstaff, Arizona. In the first hybrid generation (H1), all progeny were of a normal phenotype. Because we were also conducting an unrelated experiment with these butterflies, we crossed the H1 *bairdi* X *oregonius* hybrids with *P. polyxenes asterius* from Warsaw in Benton Co., Missouri. Again, the H2 progeny were all of a normal black phenotype. Next, the H2 (*bairdi* X *oregonius*) X *asterius* hybrids were back-crossed to the original Celilo *oregonius* stock (progeny of Or 84-1 F-2). Although some of our H3 broods produced only normal phenotypes, two crosses did yield the "cal" mutation combined with the black phenotype, and these closely resemble the original *calverleyi* specimens. We also replicated this experiment by substituting *P. joanae* from Warsaw, Missouri for the *asterius* parent in the H2 hybrid cross, and again obtained black *calverleyi*-like specimens in the H3 back-cross to Celilo *oregonius* (fig. 1).

The "cal" mutation may represent some type of deletion in the genetic information needed to produce the black wing borders in the *Papilio machaon* complex. This could result from a simple point-mutation at a control locus. However, it could also be the result of a major deletion of a chromosomal arm, perhaps even an entire chromosome. We have not yet attempted any karyotype studies to check this possibility. However, "cal" homozygotes appear to exhibit various pleiotropic and/or epistatic effects from this mutation in addition to the black wing borders. Most "cal" individuals show reduced vigor and poor fertility, while their normal siblings show normal vigor and fertility. As yet, we have only obtained two larvae from a "cal" homozygote (neither survived), and all of our breeding experiments have been conducted with heterozygote carriers of "cal". This has not been easy, because the carriers do not differ in phenotype from non-carriers. Moreover, in many family lines which produce "cal" phenotypes, there is often a sharp deficit in the number of "cal" homozygotes. For example, in one of our H3 hybrid back-crosses to Celilo *oregonius* (As-Or-Bd-Tc 86-1), 49 progeny were obtained, but only 3 were of the "cal" phenotype. This is a very significant deviation from the 3:1 ratio that we expected to obtain ($\chi^2 < .003$), and suggests that the homozygotes of "cal" may suffer exceptional mortality during development. Such deleterious effects may be expected if the mutation is the result of a chromosomal deletion.

In conclusion, the information that we have obtained in studying the "cal" mutation demonstrates the value of conducting inbreeding experiments with butterflies. First, these studies provide some insight into the recessive genetic variation carried by natural butterfly populations as

recently noted by Dimock & Mattoni (1986). Second, specific genetic variants provide insight into how the butterfly genome is structured and functions. In the case of the "cal" mutation, it provides us with the knowledge that a specific part of the genome is responsible for producing the black wing borders in the *Papilio machaon* complex, and that this segment of genetic information is independent of other parts of the genome that encode for the remaining components of the wing pattern including general coloration, submarginal spots, black discal bars, and the anal spot of the hindwing.

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The Life History of *Automeris zephyria* (Saturniidae)

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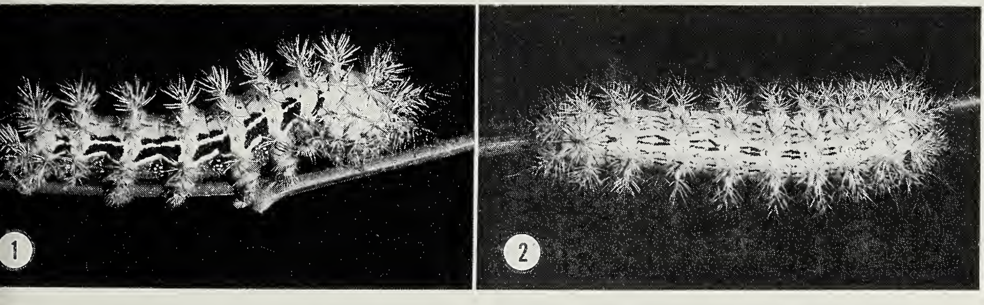
Abstract. *Automeris zephyria* occurs in the mountain ranges of central New Mexico, and a small portion of western Texas. There is one generation per year, and the adult flight season extends from mid-May to mid-July. The only confirmed natural larval host plant is *Salix*. Larvae were reared to maturity on *Cercocarpus, Cercis, Prunus,* and *Quercus*. The ground color of the mature larva is primarily yellow with a thin light blue mid-dorsal line. Pupation occurs among debris on the ground during August and September.

Introduction

Automeris zephyria Grote inhabits the central mountain ranges of New Mexico, south into the portion of the Guadalupe Mountains that extends into western Texas. Since its initial description in 1882 little information has been published on the biology of *zephyria*. Ferguson (1972), reviewed the available collecting data and illustrated the adults.

Adult *Automeris zephyria* are attracted to lights and have been captured from mid-May to mid-July, with most records from early to mid-June. In June 1985, *zephyria* was common at lights (34 ♂♂, 8 ♀♀, VI-8-9-1985) in High Rolls (Sacramento Mts., Otero Co. N.M., elev. 1993 m). The High Rolls habitat is a pinyon-juniper woodland, with scattered oaks representing elements of southwestern Madrean Evergreen Woodland (Brown 1982, Little 1976). Most trees are under 12 m in height and widely separated. A low growing *Salix* is a common member of the riparian habitat. Other *zephyria* habitats in the area were visited. Karr Canyon Picnic Ground (elev. 2430 m), 9.2 km S. of High Rolls, is coniferous woodland, while Pine Campground near Cloudcroft (elev. 2690 m) is Sierran Montane Conifer Forest habitat (Brown 1982). The mountain systems in New Mexico and Texas inhabited by *zephyria* (Sangre de Cristo, Sandia, Capitan, Sacramento, and Guadalupe) have sufficient elevation to contain the Sierran Montane Conifer Forest community. With the exception of Sitting Bull Falls in the Sacramento Mts. (elev. 1472 m), most locations where *zephyria* is collected exceed 1750 m.



Figs. 1-2. Mature sixth instar larva of *Automeris zephyria*: 1, lateral view; 2. dorsal view.

At High Rolls, both sexes were attracted to lights from about one hour after dark until observations ended at 0030 h. In captivity mating occurred after 2330 h (N = 4). Pairs remained together until nearly dawn and then separated. Oviposition began the following night. Eggs were deposited in clusters on the sides of paper bags. Due to the artificial substrate the number of eggs that would be naturally deposited in a cluster is unknown.

As with all U.S. *Automeris*, the ova are white, and when fertile, develop a black dot on the top of the egg. The only confirmed natural larval food plant is an unidentified species of *Salix* (Kenneth Hansen, pers. comm.). Since 1972, we have reared larvae on four different occasions. In captivity larvae successfully developed to maturity on *Salix* sp. (willow), *Cercocarpus betuloides* Nutt. (mountain mahogany), *Cercis canadensis* L. (redbud), and four species of Oak, *Quercus phellos* L. (willow oak), *Q. nigra* L. (water oak), *Q. oblongifolia* Torr. (Mexican Blue Oak), and *Q. alba* L. (white oak). Richard Peigler has reared *zephyria* on *Prunus serotina* Ehrh. (Donahue, 1979). Upon emergence from the eggs, larvae feed gregariously. As with other *Automeris* and *Hemileuca* species larval clusters may divide and reunite numerous times during a 24 hour period. After the fourth instar larvae tended to feed singly.

Larvae mature and pupate during late August and September (N = 108). Prior to pupation they leave the host plant and construct cocoons on the ground among debris. Based on a review of the flight data and our rearing experience, there is one generation per year. Suggestions that the two and one half month flight periods may represent two generations (Collins and Weast 1961, Ferguson 1972) appear incorrect.

Larval Description

The larval descriptions are based on material reared from ova deposited by a female collected at the Tunnel Inn, High Rolls, Sacramento Mts., Otero Co., N.M. Twenty-three larvae from Sunspot, Otero Co. and five from Dark Canyon, Guadalupe Mts., Eddy Co., N.M. were also reared to maturity and examined.

Calipers were used to measure various characters at the end of each instar. Preserved larvae are in the collection of both authors and will be deposited in an institutional collection upon completion of larval studies.

First instar. Head: Diameter 1 mm. Brown with sparse short gold setae. Body: Ground color yellowish green. Length 7.5 mm, width 1.5 mm. All scoli black. Dorsal meso- and metathoracic scoli slightly enlarged and forked. Remaining scoli appear as simple shafts. Prolegs, true legs, sublateral and ventral surfaces brownish yellow.

Second instar. Head: Diameter 1.3 mm. Reddish brown with sparse short gold setae. Body: Ground color yellowish green and reddish brown. Length 11-12 mm, width 1.6 mm. Thoracic, caudal, and dorsal abdominal scoli black with black spines. Dorsolateral scoli reduced in size with black shaft and yellow spines. Lateral and sublateral scoli reduced in size; shafts yellow with yellow spines. Dorsal area yellowish green with brownish red mid-dorsal line. Brownish red intersegmental bars in line with dorsal scoli. Lateral surface reddish brown with two thin yellowish green lines extending length of abdomen: first passes just ventral of lateral scoli; second passes through base of sublateral scoli. Prolegs, true legs, and ventral surface, red.

Third instar. Head: Diameter 1.9-2.0 mm. Dark brown with short light brown setae. Body: Ground color yellow. Length 12-15 mm, width 3 mm. Dorsal scoli with black shafts and yellow and black spines. Dorsolateral scoli similar to dorsal scoli but ½ the length. Lateral and sublateral scoli reduced in size; yellow with trace of black on some spines and shafts. Segmental area yellow with black dot between dorsal and dorsolateral scoli. Lateral intersegmental area black and crossed by numerous yellow lines that extend length of larva: first connects distal edge of each dorsal scolus; second passes mid way between dorsal and dorsolateral scoli; third passes through base of lateral scoli; fourth passes through base of each sublateral scolus. Sublateral surface black. Ventral surface brown. Prolegs, true legs, and spiracles, reddish brown.

Fourth instar. Head: Diameter 2.3-2.9 mm. Reddish brown with short white secondary setae. Body: Ground color yellow. Length 22-25 mm, width 4 mm. Dorsal scoli elongated with black shafts; spines yellow with black tips. Dorsolateral, lateral, and sublateral scoli similar, but latter reduced in size. Mid-dorsal line black. Dorsal and dorsolateral surfaces yellow with three horizontal thin black intersegmental lines. Lateral and sublateral intersegmental areas and posterior and anterior of segments black with two thin horizontal white lines: first touches base of each lateral scoli; second connects sublateral scoli; both lines disrupted by yellow segmental coloration. Lateral yellow segmental areas with small black bar between dorsolateral and lateral scoli; similar but longer black line occurs just posterior of small black bar. Ventral surface brownish red. Prolegs and true legs, red. Spiracles brown.

Fifth instar. Head: Diameter 3.7-4.2 mm. Reddish brown with short white secondary setae. Body: Ground color yellow. Length 28-35 mm, width 7 mm. Dorsal and dorsolateral scoli with black shafts and yellow spines; some spines with black tips. Lateral and sublateral scoli reduced in size, with black shafts and yellow spines. Thin mid-dorsal line bluish gray and bordered by thin black stripe. Segmental area yellow. Intersegmental area with numerous thin horizontal stripes; progressing from the outer edge of mid-dorsal line to a point even with dorsolateral scoli, series of lines as follows: yellow, black, greenish yellow, black, yellow, black, greenish yellow, black. Three well developed inter-

segmental lines extend below these to lateral scoli: first solid white, well developed, extending from abdominal segment one (Al) to (A8); second solid black intersegmental patch extends from mesothorax (T2) to A9; third white inverted "v", connecting base of lateral scoli from A2 to A7. Sublateral and ventral surface black with a few white pinacula. Ventral intersegmental area black or red. Prolegs red, with red patch posterior to upper portion of leg. True legs, red. Spiracles light brown.

Sixth instar. Head: Diameter 4.9-5.9 mm. Frons black, adfrontal area and clypeus brown. Body: Ground color yellow. Length 46-57 mm, width 9-10 mm. Dorsal, dorsolateral, and lateral scoli shaft with black tips and yellow base; spines predominantly yellow, some with black tips. Sublateral scoli yellow. Mid-dorsal line bluish gray and bordered on each edge by thin black stripe. Segmental area yellow. Lateral and dorsal lateral abdominal surfaces with yellow, black, greenish yellow and white stripes as in fifth instar. A red patch with white pinacula and short white secondary setae occurs both posterior and anterior of upper proleg base. Ventral surface black with white pinacula. Mid-ventral area reddish. Prolegs and true legs red. Spiracles light brown.

The larvae of *zephyria* differ markedly from those of *A. cecrops pamina* (Neum.). Although their shapes are similar, mature *pamina* larvae are light gray-green with a few thin white, grayish, and black lines on the dorsal and dorsolateral surfaces. On the lateral surface, *pamina* has two prominent diagonal white lines that converge as they reach the lateral scoli of the succeeding segment. In *zephyria*, these two corresponding white lines are roughly parallel (Figs. 1 & 2). The ground color of the mature larva is yellow and there are numerous prominent yellow, light green, black, and yellowish green lateral lines present on the dorsolateral and lateral surfaces. At present, there is no indication that these two species occur sympatrically. *Automeris io neomexicana* B. & Benj. also occurs in New Mexico, but their larval ground color is green with a red and white lateral line extending the length of the abdomen. Thus, *zephyria* larvae are easily separated from related species. A key to the last instar *Automeris* larvae of the United States (Tuskes 1986) and color larval illustration of *zephyria* and *io* (Donahue 1979) and *cecrops pamina* (Packard 1914) have been published.

Acknowledgements. We thank Peter Jump, Kenneth Hansen, Jim Coleman and Noel McFarland for records, and Michael Collins and Richard Peigler for suggestions on the manuscript.

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Three new species of *Paradirphia* (Saturniidae: Hemileucinae) from Mexico and Central America with notes on the immature stages

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Abstract. Observation of the early stages and subsequent study of the genitalia revealed that, in addition to *P. semirosea* and *P. coprea*, three new species are involved in the *P. semirosea* complex in Mexico and Central America. *P. semirosea* and *P. coprea* are redescribed and lectotypes are designated. *P. boudinoti* and *P. valverdei* are described from northeastern and southern Mexico, respectively, and *P. winifredae* from Costa Rica and Panama. Type specimens are figured and male and female (when known) genitalia of the five species are illustrated. Species distribution is discussed and mapped. The immature stages of *P. semirosea*, *P. boudinoti* and *P. valverdei* are described with reference to larval food preferences in the laboratory.

Introduction

Paradirphia, with *Phricodia coprea* Draudt as type species, was originally described by Michener (1949: 146) as a subgenus of *Ormiscodes* Blanchard. Nine species were later included in the subgenus by Michener (1952: 445) in his major work on the Saturniidae of the Western Hemisphere. *Paradirphia* was then cited at full generic rank by Beutelspacher (1978, 1984) and Lampe (1986). The new status is entirely justified based on obvious differences in the general appearance and distinctive characters in the genitalia.

Paradirphia ranges from Mexico to Bolivia; it is mostly, if not exclusively, a montane genus, *P. geneforti* (Bouvier) ranging up to 2800 m in N Ecuador. It is represented by 10 species (including the new ones) in Mexico and Central America and three in South America where it is an exclusive inhabitant of the Andes. This paper was initiated by the junior author's observation of marked variability in the larvae of moths in which the wing pattern is so similar that all were originally believed to be *P. semirosea* (Walker). Subsequent study of the genitalia revealed that three species were involved in the reared material; further investigations led to evidence of at least four species in the *P.*

semirosea/P. coprea complex in Mexico, two hitherto unpublished. A third new species from the same group was found among specimens from Costa Rica and Panama.

Paradirphia semirosea and *P. coprea* will be redescribed prior to descriptions of the new taxa.

Paradirphia semirosea (Walker)

(figs. 1, 2, 3, 11, 13, 16, 17, 18, 23, 24)

Dirphia semirosea Walker, 1855: 1359
Phricodia semirosea Walker; Draudt, 1930: 781
Dirphia semirosea Walker; Bouvier, 1935: 256
Dirphia semirosea Walker; Hoffmann, 1942: 243
Ormiscodes (Paradirphia) semirosea (Walker); Michener, 1952: 445

Phricodia semirosea ab. *roseana* Draudt, 1930: 781 (infrasubspecific name)

The species cited by Lampe (1986: 273) as *P. semirosea* is *P. boudinoti* n. sp. (see below).

Male. Head dark brown, labial palpi three-segmented, dark brown, usually scattered with purplish scales. Antennae pale stramineous, quadripectinate to the apex; apical rami shorter than basal rami, those of outer side less than one-third as long as those of the inner side of flagellum. Thorax covered with brown to red brown hairs intermixed with longer gray hair-like scales on the tegulae; legs dark brown, densely scattered with carmine red; epiphyses large, covered with long hairs, about as long as two thirds of the tibia; a single subapical spur on metathoracic tibia. Abdomen dorsally black, broadly ringed with carmine red, ventrally dark brown with intermixed carmine scales. Forewing above brown, more or less suffused with purplish, especially on lower half of baso-median area and both sides of submarginal band; veins and fringes brown; lines cream white, angled as shown in figs. 1, 2, and 3, the antemedian three-sectioned, the postmedian usually continuous, emphasized with white dots at the intersection of the veins. Forewing below dark brown, more or less suffused with purplish; postmedian line straight, shaded with brown. Hindwing above purplish, in some specimens darkened with blackish brown especially on baso-median area; postmedian line black with two small, usually fused, subcostal white spots. Hindwing below about same coloration as above; postmedian line white, usually strongly contrasting, with or without white dots. The absence of discal spots is a characteristic wing pattern feature of the *P. semirosea* group. Length of forewing 30-35 mm.

Female. Antennae shortly bipectinate to the apex. Epiphysis absent. Ground color usually lighter than in male with an extension of the lightest areas tending toward purplish pink or pink instead of purplish. Averaging larger than the male; forewing 35-40 mm.

P. semirosea is the most variable of the five species studied. Pink forms were named by Draudt (1930:781) aberration *roseana*. Provisions of the Code do not apply to this name published at an infrasubspecific rank (Art. 45a). The markings also vary, especially the postmedian lines, above and below.

Male genitalia (figs. 18A, B, 23A). Uncus down-curved apically, simple, slightly notched at the apex. Valves very broad, trilobed, the lower portion of the proximal lobe connected to the transtilla; a very strong spine, posteriorly produced, arising from the inner side of the valvula. Lateral arms of the transtilla medially fused in a strongly sclerotized subtrapezoidal ventral plate. Juxta deeply concave, broadly fused to the anterior portion of the valves with lateral sides posteriorly produced as strongly sclerotized processes. Aedeagus straight; the vesica has a strong hook-like cornutus.

Female genitalia (fig. 18C). Sclerotization of the eighth sternum post-vulvar with medial portion posteriorly prominent and laterally fusing to the eighth sternum and to the anapophyses. Sclerotization of the eighth tergum bilobed. Ductus bursae chitinized; pyriform bursa moderately bulky; ductus seminalis arising from the right side very close to the ductus bursae. Postapophyses slightly longer than the anapophyses. Ovipositor well developed, covered with fine setae.

Types. *P. semirosea* was described by Walker (1855: 1359) from one male and one female. The male is hereby designated as the lectotype.

Lectotype: One male, locality unknown (43-58 = presented in 1853 by E. Doubleday Esq.) (genit. preparation D. Goodger) (British Museum, N. H.) (examined).

Distribution (fig. 24). MEXICO. VERACRUZ: 62 mi (100 km) SW of Nautla, 1290 m; Las Minas, 1385 m; Naolinco de Victoria; Orizaba, 1243 m. CHIAPAS: San Cristóbal de Las Casas, 2160 m; Oxchuc; 11 mi (18 km) W of Ocosingo, 1375 m; Pinola; Santa Rosa Comitán; Zapalota (= La Trinitaria); Las Delicias. OAXACA: 52mi (84km) NE of Guelatao, 1400m, El Portillo del Rayo, 1450 m. GUATEMALA. ALTA VERAPAZ: Mpio. San Cristóbal Verapaz, Hacienda Baléu, 1850 m; Cobán, 1200 m; BAJA VERAPAZ: Pantic, 1600 m; Santa Elena (La Cumbre); NE of Volcán Acatenango, 2200 m. COSTA RICA. CARTAGO: Tapantí, 1400 m; Moravia de Chirripó, Platanillo, 1150 m; *id.*, Tausito, 1200 m; Cantina de Río Macho, 1200 m.

P. semirosea is the most widely distributed species of *Paradirphia* in Central America where it is mainly recorded from moderate elevations from 1100 to 1500 m. The absence of records between Guatemala and Costa Rica is probably due to lack of collecting rather than to a gap in distribution.

Immature stages. See under group heading, also figs. 11, 13, 16, 17.

Material examined. Large series from the above cited localities; 22 specimens dissected.

Paradirphia coprea (Draudt)

(figs. 9, 10, 19, 24)

Phricodia coprea Draudt, 1930: 781
Dirphia coprea Draudt; Bouvier, 1935: 258
Dirphia coprea Draudt; Hoffmann, 1942: 243
Ormiscodes (Paradirphia) coprea (Draudt); Michener, 1949: 146
Ormiscodes (Paradirphia) coprea (Draudt); Michener, 1952: 445

Male. Antennae noticeably shorter than in *P. semirosea*, stramineous. *P. coprea* differs from *P. semirosea* mainly by the more uniform, duller brown of the

wings above and below as a result of less contrast between the light and dark areas, especially on the baso-median and the postmedian areas of the forewing. The markings are as in *P. semirosea*, but the postmedian line is less continuous, tending to fade between the dots on the veins. Forewing (lectotype) 38 mm.

Female. Same coloration and markings as in male. Forewing (paralectotype) 38 mm.

Male genitalia (fig. 19A, B). Differ from those of *P. semirosea* by the much shorter lateral sides of the juxta which are not posteriorly produced in strongly sclerotized processes, and in the extreme reduction of the cornutus. However, in some specimens doubtfully referred to this species (see distribution) a small hook-like cornutus is present.

Female genitalia (fig. 19C). The single specimen examined (paralectotype) presented a weaker structure than in *P. semirosea* with the bursa much smaller; the anapophyses are noticeably shorter than in the previous species.

Types. *P. coprea* was described by Draudt (1930: 781) according to three pairs from Cuernavaca, Mexico, all in his own collection. As the latter was destroyed during the Second World War, there was little hope of finding syntypes to identify this species with certainty. A search among museums where Draudt's type material is occasionally found (Museum für Naturkunde der Humboldt-Universität zu Berlin, British Museum (N.H.), Musée d'Histoire naturelle de la ville de Genève) was unsuccessful, but one male and one female syntypes were located in the American Museum of Natural History, specimens from the collection of the late Frank Johnson who probably purchased them from Draudt or Niepelt. Several other types of Saturniidae from the same source are likewise preserved. The male syntype is hereby designated as the lectotype, the female as paralectotype. Both were examined, and although old and somewhat faded (figs. 9, 10), still show the main characters of the wing pattern.

Lectotype: One male, Mexico, Morelos, Cuernavaca, VI.1912, n° 263, genit. preparation (in glycerine) C. Lemaire, n° 5217 (coll. Draudt, coll. Frank Johnson, American Museum of Natural History). Paralectotype: one female, same locality and collections, VII. 1909, n° 264, genit. preparation C. Lemaire, n° 5218.

Distribution (fig. 24). MEXICO: Type locality. The distribution as reported by Hoffmann (1942: 243): "Tierra templada de la cuenca superior del Río Balsas, Morelos, Sierra Volc. Transversal (hasta 2000 m). Jalisco" may refer to several different species. Specimens from the following localities are doubtfully identified as *P. coprea*: STATE OF MEXICO, Malinalco. GUERRERO, vicinity of Acuitlapan, 10 mi (16 km) NE of Taxco, 5000 ft (1524 m). OAXACA, Candelaria Loxicha, 550 m. In these specimens, unlike the lectotype, the vesica has a small hook-like cornutus. Although they do not otherwise differ, their identification will remain uncertain until additional topotypical material is available for comparison.

Immature stages. Unknown.

Material examined. Lecto- and paralectotype and seven questionable specimens; all dissected.

Paradirphia valverdei Lemaire & Wolfe **new species**

(figs. 4, 12, 15, 20, 24)

Male. Antennae more rusty yellow than in both previous species. Long hair-like scales of tegulae black, little intermixed with gray. Ground color of wings

above and below much darker brown than in *P. coprea*, almost black, with shades of purplish brown scarcely contrasting and confined to both sides of submarginal band on forewing and postmedian area of hindwing. Lines pure white and very contrasting; postmedian of forewing reduced to dots on the veins. Forewing length: 37-40 mm (holotype = 40 mm).

Female. The very damaged single known example (progenitor of the larvae) was unfortunately lost. It was collected at light in Veracruz, 62 mi (100 km) SW of Nautla, 1290 m, 1.VIII.1984, K. Wolfe, M. Valverde.

Male genitalia (fig. 20). A much larger structure than in *P. coprea*. Shape of valves differing with inner lobe (fused to the transtilla) larger, and posteriorly oriented spine noticeably stronger. Lateral sides of juxta more prominent than in *P. coprea* but not as much as in *P. semirosea*, and less sclerotized as in latter; connection of juxta to anterior protion of valves differs from *P. semirosea* (figs. 18, 23A). Cornutus minute or entirely lacking from vesica.

Types. Holotype: male, Mexico, Oaxaca 52 mi (84 km) NE of Guelatao, 1400 m, 27.VII.1987, K. Wolfe, M. Valverde, D. Mullins. Paratypes: two males, same locality, data and collectors; five males, 53 mi (85 km) NE of Guelatao, 1475 m, 30.VII.1984, K. Wolfe, M. Valverde; one male, Oaxaca, 45 mi (72 km) NE of Guelatao, 2000 m, 29.VII.1984; four males, Oaxaca, 54 mi (87 km) SW of Tuxtepec, 1260 m, 25.VII.1984, same collectors; one male, Veracruz, 62 mi (100 km) SW Nautla, 1290 m, 3.VIII.1984, same collectors.

The holotype and three paratypes are in the collection of the Muséum national d'Histoire naturelle, Paris, five paratypes are in the collection of the junior author, one paratype is in the San Diego Natural History Museum, one paratype each will be deposited in the Natural History Museum of Los Angeles County, the American Museum of Natural History, the Allyn Museum of Entomology, Sarasota, Florida, and the Colección Entomológica del Instituto de Biología de la Universidad Nacional Autónoma de México.

Distribution (fig. 24). *P. valverdei* is known only from the above cited localities at moderate elevations in Oaxaca and Veracruz where it is sympatric and synchronic with the more numerous *P. semirosea*.

Immature stages. See under group heading, also figs. 12, 15.

Material examined. 14 males; seven dissected.

This species is named after Marvin D. Valverde to show gratitude for his contribution to the collecting and the rearing of the material studied.

Paradirphia boudinoti Lemaire & Wolfe **new species**

(figs. 7, 8, 14, 21, 24)

Male. Antennae straw yellow. Like *P. coprea* and *P. valverdei*, this species differs from *P. semirosea* by the reduction of contrast between light and dark areas on wings above and below. Coloration not as dark as in *P. valverdei*, and one specimen from Mexico, Coahuila, Saltillo, with the purplish as contrasting as in lectotype of *P. semirosea*. Lines cream white as in *P. semirosea*, postmedian of forewing usually reduced to vein-dots but, in some specimens, as continuous as in *P. semirosea*. Forewing 33-36 mm (holotype = 35 mm).

Female. Slightly larger than male, same markings and coloration. Forewing (allotype) 40 mm.

Male genitalia (fig. 21A, B). Distinguished from three previous species by hypertrophy of inner lobe (fused to transtilla) and much longer spine of valves. Lateral sides of juxta not prominent as in *P. coprea*. Most characteristic feature

Table 1. Larval description of *Paradirphia*. *P. semirosea*, *P. boudinoti*, *P. valverdei*, sixth (last) instar.

	P. semirosea	P. boudinoti	P. valverdei
Head (0.5 mm)	orange, adfrontal sutures black	coral pink, adfrontal sutures black	blue green, adfrontal sutures black
Integument:			
—Dorsal and lateral areas	red-brown, speckled whitish	yellow, densely covered with black vermiculations	light green, broadly but indistinctly checkered with red
—Ventral area	duller, similar	similar	blue green
Dorsal band	broad, dark brown	almost inconspicuous, white	greenish white
Subdorsal, upper and lower sub-spiracular lines	white	greenish white	white
Spiracular band	dark brown	denser black markings	copper red
Subspiracular band	white	white	white
Thoracic legs	orange	orange	pale green
Abdominal legs	brown	black	blue green tipped with black
Anal plate	pink surrounded with black	orange	blue-green
Paranal lobes	pink surrounded with black	orange thinly surrounded with black	blue green surrounded with black
Spiracles	orange surrounded with black, then white	chestnut brown circled with black, then orange white	orange circled with white
Scoli	rusty orange brown, prothoracic spines, dorsal and subdorsal spines of abdominal segment 9 black	orange, spines orange interspersed with black	green, prothoracic spines, dorsal and subdorsal spines of abdominal segment 9 black

of armature is wedge-like shape of aedeagus; vesica lacking cornutus.

Female genitalia (fig. 21C). Differing from *P. semirosea* and *P. coprea* by less prominent medial portion of ventral plate. Narrow prevulvar belt present in both dissected specimens. Bursa noticeably bulkier than in *P. semirosea*.

Types. Holotype: male, Mexico, Tamaulipas, Gómez Farias, Rancho del Cielo, 1127 m, 8-11.V.1985, J. Boudinot. Allotype: female, same locality, dates and collector. Paratypes: eight males, one female, same locality, dates and collector; 18 males, San Luis Potosí, Ciudad del Maíz, E1 Platanito, Torre Forestal, 1160 m, 26.VII-1.VIII.1984, E. C. Welling (all in the Muséum national d'Histoire naturelle, Paris); two males, San Luis Potosí, 16 mi (26 km) E of Ciudad del Maíz, 1140 m, 2.VII.1983, K. Wolfe, M. Valverde (K. Wolfe collection); one male, San Luis Potosí, E1 Naranjo, 5.VIII.1975, T. W. Taylor (Natural History Museum of Los Angeles County); five males, five females, Puebla, Villa Juárez; four males, Puebla, San Juan Apulco (Allyn Museum of Entomology, Sarasota). One paratype each will be deposited in the American Museum of Natural History and in the Colección Entomológica del Instituto de Biología de la Universidad Nacional Autónoma de México.

Distribution (fig. 24). *P. boudinoti* is widely distributed in NE Mexico from Coahuila to Puebla, its southernmost range meeting the northernmost of *P. semirosea*. Additional records are from COAHUILA, Saltillo, 1599 m, and HIDALGO, 70 mi (113 km) S of Tamazunchale, 1700 m. *P. boudinoti* probably lives in drier areas than *P. semirosea*.

Immature stages. See under group heading, also fig. 14.

Material examined. 32 specimens; 11 dissected.

This species is named after Jacques Boudinot of the Department of Entomology of the Muséum national d'Histoire naturelle, Paris, to express gratitude for the collecting of a great part of the type material during his mission to Mexico in July and August 1985.

Paradirphia winifredae Lemaire & Wolfe **new species**

(figs. 5, 6, 22, 23, 24)

Male. Antennae straw yellow. Red scales on thorax and legs, dorsal rings on abdomen paler pink, not carmine as in four previous species. Ground color dark gray brown as in *P. boudinoti*; purplish zones on forewings confined to postmedian area, especially between postmedian line and submarginal band

Fig. 1. *Paradirphia semirosea* male, Mexico, Veracruz, Las Minas, 1385 m, *ab ovo*, Escondido, California, on *Robinia pseudoacacia*.

Fig. 2. *Paradirphia semirosea* female, Chiapas, 11 mi. (18 km) W. of Ocosingo, 1375 m, 21.VII. 1987 (K. Wolfe, M. Valverde, D. Mullins).

Fig. 3. *Paradirphia semirosea* male (extreme pink phase), Chiapas, 15 mi (25 km) W of Ocosingo, 1325 m, 10.VIII.1985 (K. Wolfe, M. Valverde).

Fig. 4. *Paradirphia valverdei* new species, paratype male, Mexico, Oaxaca, 52 mi (84 km) NE of Guelatao, 1400 m, 27.VIII.1987 (K. Wolfe, M. Valverde, D. Mullins).

Fig. 5. *Paradirphia winifredae* new species, paratype male, Costa Rica, Cartago, Tapantí, 1540 m, 10.VII.1988 (K. Wolfe, M. Valverde).

Fig. 6. *Paradirphia winifredae* new species, paratype female, Costa Rica, Cartago, El Empalme, 2000 m, 6.IV.1978, (K. Wolfe, M. Valverde).

Fig. 7. *Paradirphia boudinoti* new species, paratype male, San Luis Potosí, 16 mi (27 km) E of Cd. Maíz, 1140 m, 2.VII.1983 (K. Wolfe, M. Valverde).

Fig. 8. *Paradirphia boudinoti* new species, allotype female, Mexico, Tamaulipas, Gómez Farias, Rancho del Cielo, 1127 m, 8/11.1985 (J. Boudinot) (Muséum national d'Histoire naturelle, Paris).

Fig. 9. *Paradirphia coprea* lectotype male, Mexico, Morelos, Cuernavaca, VI.1912 (American Museum of Natural History).

Fig. 10. *Paradirphia coprea* paralectotype female, same locality, VII. 1909 (American Museum of Natural History).

Fig. 11. First instar larvae of *Paradirphia semirosea* (similar to first instar of *P. valverdei* and *P. boudinoti*), Mexico, Chiapas, 18 mi (29 km) W of Ocosingo, *ab ovo*, Escondido, California, on *Robinia pseudoacacia*.

Fig. 12. Fourth instar larva of *Paradirphia valverdei* (similar to fourth instar of *P. semirosea* and *P. boudinoti*), Mexico, Veracruz, 62 mi (100 km) SW of Nautla, 1290 m, *ab ovo*, Escondido, California, on plum.

Fig. 13. Larva of *Paradirphia semirosea* sixth (last) instar, Mexico, Chiapas, 11 mi (18 km) W of Ocosingo, 1375 m, *ab ovo*, Gordes (France) on *Robinia pseudoacacia*.

Fig. 14. Larva of *Paradirphia boudinoti* sixth (last) instar, Mexico, Hidalgo, 70 mi S of Tamazunchale, 1700 m, *ab ovo*, Escondido, California, on *Robinia pseudoacacia*.

Fig. 15. Larva of *Paradirphia valverdei* sixth (last) instar, same data as fig. 12.

Fig. 16. Eggs of *Paradirphia semirosea*, Mexico, Chiapas, same data as fig. 13.

Fig. 17. Pupae of *Paradirphia semirosea*, same data as above.


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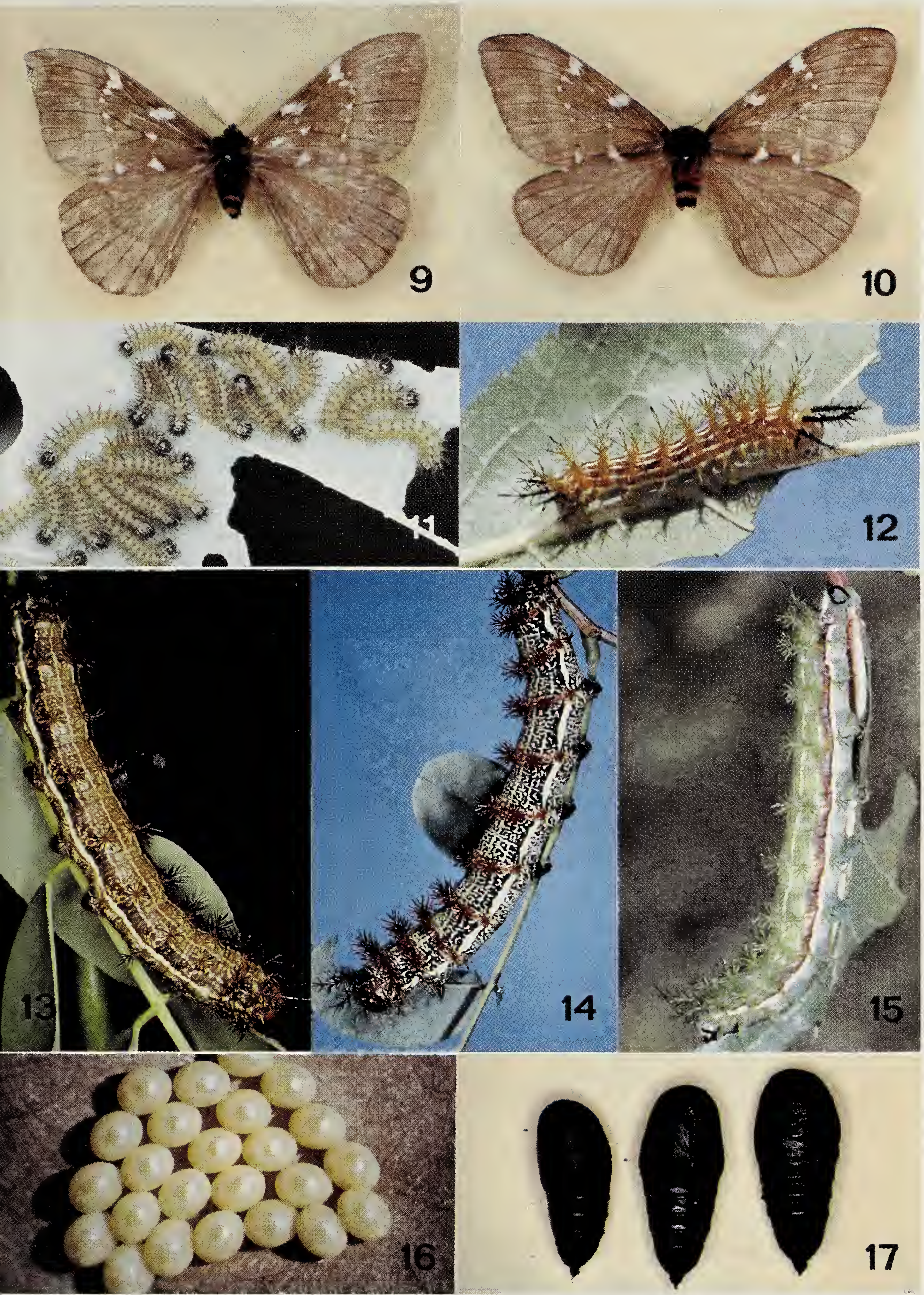
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where they form a contrasting, well delineated band from costa to inner margin. Lines less conspicuous than in all previous species, postmedian usually reduced to white vein-dots, the one on the inner margin line being as small as those on veins Culb to M1. *P. winifredae* averages larger than *P. semirosea*. Forewing 34-39 mm (holotype = 39 mm) versus 31-35 mm in examined *P. semirosea* males from Costa Rica.

Female. Larger and darker than male, with purplish brown zone on forewing proximal to submarginal band less conspicuous. White vein-dots on ante- and postmedian lines especially small, except subcostal. Forewing (allotype) 40 mm.

Male genitalia (figs. 22A, B, 23B). Resembling those of *P. semirosea* in having lateral sides of juxta well prominent. Differing in shape of valves and in connection of inner portion of valves to juxta, as shown in fig. 23. Vesica has strong hook-like cornutus as in *P. semirosea.*

Female genitalia (fig. 22C). Same structure as in *P. semirosea.*

Types. Holotype: male, Costa Rica, Cartago, Tapantí, 1660 m, 22.VIII.1984, F. Bénéluz (genit. preparation in glycerine, C. Lemaire, n° 5075). Allotype: female, Costa Rica, Puntarenas, Monteverde, Río Guacimal, Nuboso, 1550 m, 8.IX.1983, J.-M. Cadiou, W. Haber (genit. preparation in glycerine, C. Lemaire, n° 5102). Paratypes: two males, Cartago, Tapantí, 1600 m, 8.VI., 15.XII.1985, F. Bénéluz, Muséum national d'Histoire naturelle, Paris; one male, Cartago, Tapantí, 1540 m, K. Wolfe, M. Valverde; one female, Cartago, El Empalme, 2000 m, 6.VIIII.1978, same collectors (collection of junior author); two males, Alajuela, Volcán Poás, 2350 m; one male, Cartago, 16 km S of Cartago on Pan American Highway, 1800 m; one male, Puntarenas, Monteverde, 1300 m; two males, San José, Parque Nacional Braulio Carillo, Estación Zurquí, 1500 m (collection of the University of Pennsylvania, Philadelphia); 15 males, Panama, Santa Clara de Chiriquí, 1600 m, 5.VI.1968, C. Moinier (Muséum national d'Histoire naturelle, Paris). One paratype each will be deposited in the Natural History Museum of Los Angeles County, the American Museum of Natural History, and the Allyn Museum of Entomology.

Distribution (fig. 24). In addition to the above cited localities, there are records from Panama, Chiriquí, road from Gualaca to Fortuna, km 32, Hornito, 1000 m; El Hato del Volcán, Quebrada Tisingal, 1400 m; Boquete, Alto Quiel, 1700 m. Although occurring in neighboring areas, *P. winifredae* and *P. semirosea* are probably allopatric or only occasionally sympatric. In Monteverde, Costa Rica, where both species occur in the same area of montane rainforest, *P. winifredae* has been collected at higher elevations than *P. semirosea.*

Immature stages. Unknown.

Material examined. 36 specimens; 18 dissected.

This species is named after Winifred Hallwachs, for her contributions to the knowledge of the Saturniidae of Parque Nacional Santa Rosa, Guanacaste, Costa Rica.

Immature stages (*P. semirosea, P. boudinoti, P. valverdei*)

Egg (fig. 16). Diameter ca. 1.5 mm, yellow to greenish yellow, becoming gray about five days before hatching.

Larva (Figs. 11-15). Length ca. 2.5 mm (first instar) to 65-70 mm

(last instar). There are six instars (five molts) and spination and pattern of markings are typically hemileucine. The arrangement of scoli is as in *Leucanella leucane* (Geyer) (see Lemaire, 1971: 30), and is as follows: Thoracic segments, abdominal segments 1, 2, 7 bear four pairs (subdorsal, prespiracular, upper and lower subspiracular); abdominal segments 3-6, three pairs (lower subspiracular absent); abdominal segment 8 has subdorsal pair fused into a single dorsal scolus + three pairs as in abdominal segment 7; abdominal segment 9 has dorsal scolus as in segment 8, but removed to posterior end of segment + three pairs (upper subdorsal, lower subdorsal, subspiracular); abdominal segment 10 has paranal scoli present. In the first instar, subdorsal and prespiracular pairs on thoracic segment and dorsal scolus on abdominal segments 8 and 9 are apically forked.

There are usually distinctive generic characters in the larvae of Hemileucinae, such as the rosette-type dorsal scoli in *Hemileuca* and the hypertrophied upper subdorsal scolus of abdominal segment 9 in *Periphoba* (see Gardiner, 1982: 145, *P. arcaei*, figured as "*P. hircia*"). The most characteristic features in the larvae of *Paradirphia* studied are 1) the absence of obviously predominant scoli, and (2) the slightly longer subdorsal and prespiracular scoli on the prothoracic segment and longer lower subdorsal pair on abdominal segment 9. Structure of the different groups of scoli is unusually indistinct.

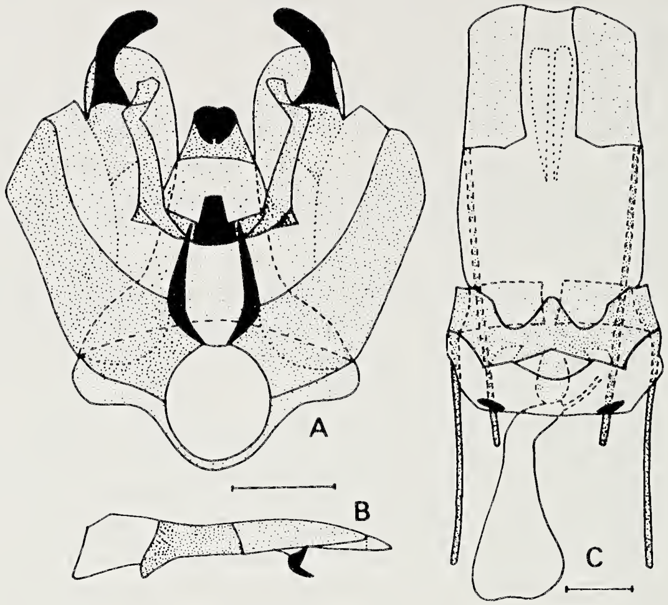
There are distinctive specific characters in the larvae of *Paradirphia* which were studied, especially in the color of the integument; sixth instar larvae of *P. semirosea*, *P. valverdei*, and *P. boudinoti* are respectively orange and brown, green and red, and yellow and black.

Lampe (1986: 273) described the immature stages of *P. boudinoti* logically referring to them as *P. semirosea*, unaware of the features which gave rise to this study.

A comparative description of the 6th instar larvae of *P. semirosea*, *P. valverdei*, and *P. boudinoti* is given in table 1.

Pupa (fig. 17). Unlike most of the Hemileucinae, the larvae of the species of *Paradirphia* reared do not spin cocoons. Before pupation, the larvae leave the plant in search of a pupation site. There are no traces of silk in the pupal chamber formed in the soil at a depth of 10 cm or more. The pupa of *P. semirosea* is ca. 30 mm long, black and smooth, with thoracic segments rounded. Cremaster is simple, prominent, bearing a tuft of strong hooks at the anal end.

Larval hostplant preferences (in the laboratory). *P. semirosea* preferred *Robinia pseudoacacia* (Leguminosae) over a variety of other plants offered in California and France; *P. boudinoti* accepted plum (*Prunus*: Rosaceae) in France, plum and *R. pseudoacacia* in California, and *Malus* (Rosaceae) in Germany; *P. valverdei* preferred plum in California. Native host plants are unknown.



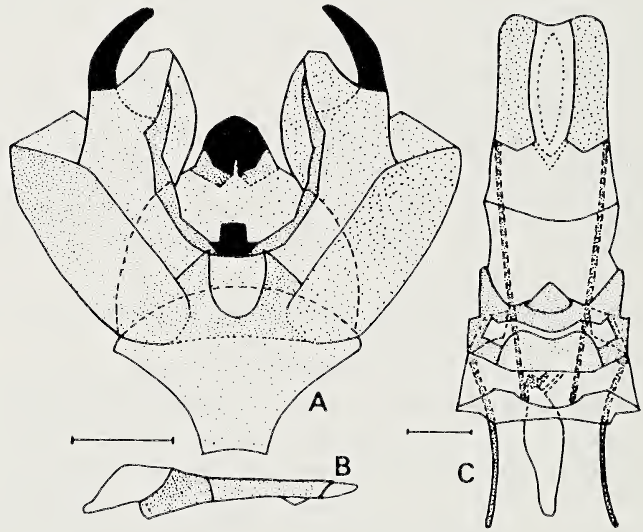
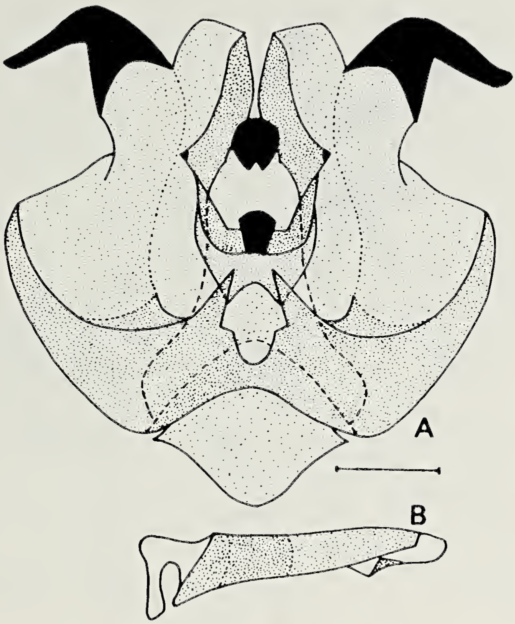


Fig. 18. Genitalia of *Paradirphia semirosea*. A. Male, aedeagus removed, ventral view; B. Aedeagus, lateral view; C. Female, ventral view, Scale line = 1 mm.

Fig. 19. Genitalia of *Paradirphia coprea*. A. Male (lectotype), aedeagus removed, ventral view; B. Aedeagus, lateral view; C. Female (Paralectotype), ventral view. Scale line = 1 mm.



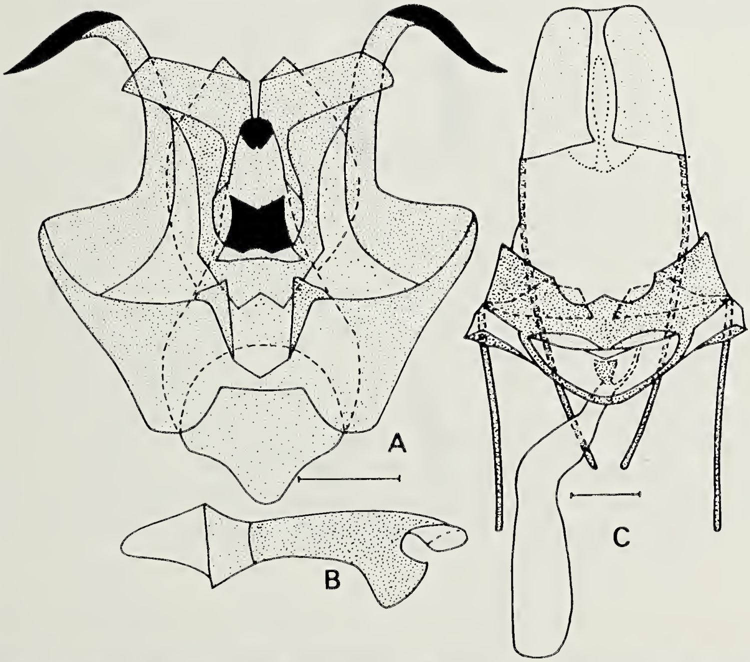
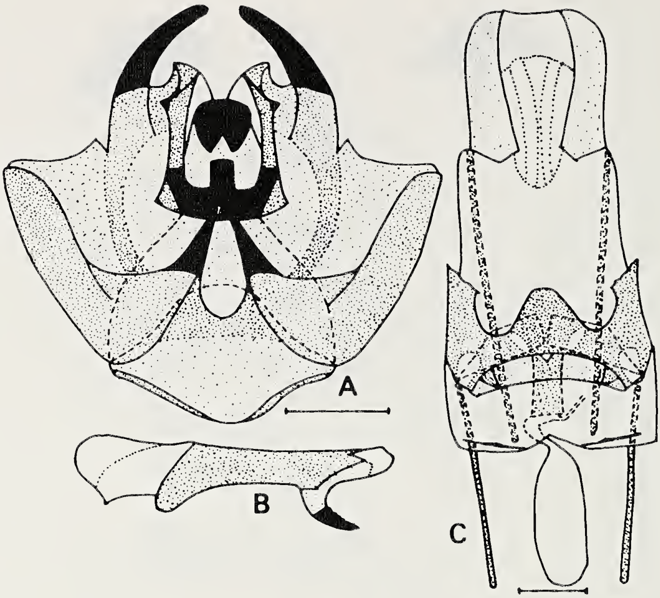


Fig. 20. Male genitalia of *Paradirphia valverdei* new species. A. Aedeagus removed, ventral view; B. Aedeagus, lateral view. Scale line = 1 mm.

Fig. 21. Genitalia of *Paradirphia boudinoti* new species. A. Male, aedeagus removed, ventral view; B. Aedeagus, lateral view; C. Female, ventral view. Scale line = 1 mm.



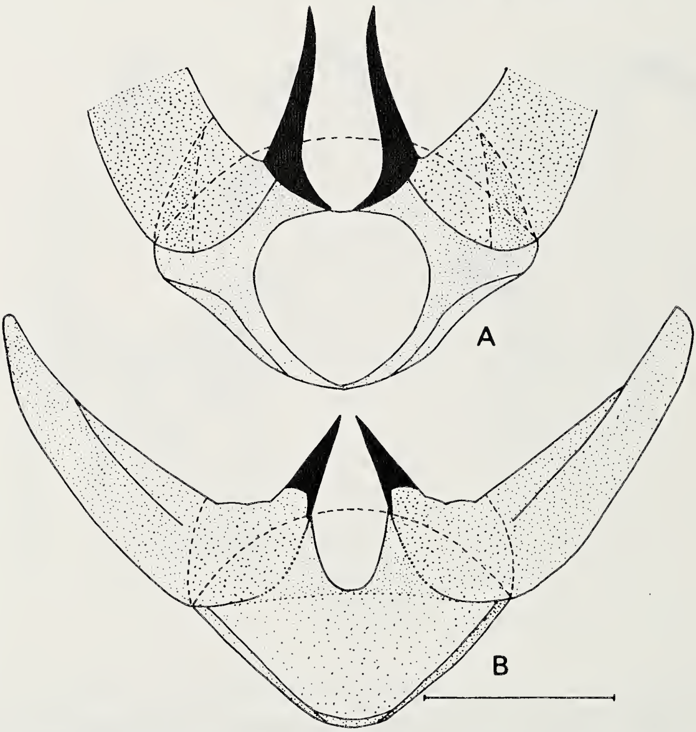


Fig. 22. Genitalia of *Paradirphia winifredae* new species. A. Male, aedeagus removed, ventral view; B. Aedeagus, lateral view; C. Female (allotype), ventral view. Scale line = 1 mm.

Fig. 23. Juxta and anterior portion of the valves in genitalia of *Paradirphia*. A. *P. semirosea*; B. *P. winifredae*. Scale line = 1 mm.

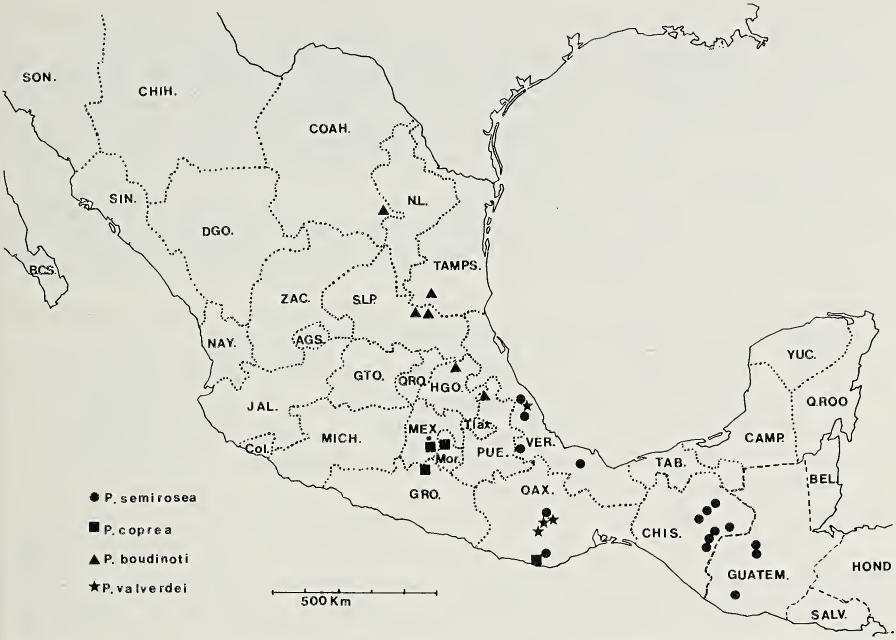


Fig. 24. Geographical distribution in Mexico and Guatemala of the species of *Paradirphia* studied.

Acknowledgements. We thank F. H. Rindge (American Museum of Natural History) for the loan of the syntypes of *P. coprea* of which the identification was thus made possible. A. Watson and D. Goodger (British Museum (Natural History) kindly dissected the genitalia and confirmed the identification of the lectotype of *P. semirosea.* Equally we thank H. J. Hannemann (Museum für Naturkunde der Humboldt Universität zu Berlin), J. Donahue (Natural History Museum of Los Angeles County), D. H. Janzen, (Department of Biology, University of Pennsylvania) and L. and J. Miller (Allyn Museum of Entomology of the Florida State Museum) for the loan of specimens. F. Bénéluz, J.-M. Cadiou, W. Haber, W. Hallwachs, D. H. Janzen, R. Lampe, C. Moinier, D. Mullins, T. Porion, L. Schwartz, M. Valverde and N. Venedictoff have either collected or reared the studied material. Thanks also to R. S. Peigler and two anonymous reviewers for their helpful comments and suggestions.

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Journal of Research on the Lepidoptera 27(3-4):213-221, 1988(89)

A List of the Butterflies and Skippers of Mount Revelstoke and Glacier National Parks, British Columbia, Canada (Lepidoptera)

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Abstract. An annotated list of 63 species of butterflies and skippers found in Mount Revelstoke and Glacier National Parks, British Columbia, Canada, has been complied. Eight additional species are considered to be likely additions to the known fauna, and one previous record to be a mislabelled European specimen. The alpine species present on the two highest peaks near Revelstoke are also listed.

Introduction

Mount Revelstoke and Glacier National Parks are located west of the Rockies in the Columbia Mountains of southeastern British Columbia, Canada. The Monashee, Selkirk, and Pucell Ranges form the portion of the Columbia Mountains in the vicinity of the parks. Mount Revelstoke National Park (M.R.N.P. henceforth) encompasses 25,900 hectares and is located in the western part of the Selkirk Mountains. It is approximately bounded by latitudes 51°00′-51°15′ North, longitudes 117°50′-118°15′ West. Glacier National Park (G.N.P. henceforth) encompasses 135,000 hectares and is located in the Selkik and Purcell Ranges, with the Beaver River Valley separating the two ranges in the park. G. N. P. is bounded by latitudes 51°00′-51°30′ North, longitudes 117°10′-118°00′ West. The town of Revelstoke lies at the southwest edge of M.R.N.P. on the Columbia River between the Monashee and Selkirk Ranges.

Other than a small amount of collecting by Mark Hobson and John G. Woods, no previous study has been conducted on the butterflies of these parks. The reason for the paucity of collecting is probably the inhospitable climate and terrain. The mountains rise precipitously from the deep valley floors (450 m) up to a maximum of 3387 m elevation. The only access roads are the Trans-Canada Highway (which skirts M.R.N.P. and bisects G.N.P.) and a road to the summit of Mt. Revelstoke. Many of the mountain trials are long and strenuous to climb. Dense coniferous forest (Columbia Forest 456-1220 m, subalpine forest above 1220 m) covers most of the area below treeline, with the only breaks in the forest being due to cliffs, streams, avalanches, and the activities of man. Treeline is at about 1800-2000 m or occasionally higher, above

Annual precipitation in the parks is generally 150-200 cm, but parts of G. N. P. receive up to 350 cm. Much of the precipitation occurs in the

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winter, resulting in heavy snow packs which are slow to melt. Summers are generally warm with frequent cool rainly intervals. At the lower elevations (Columbia River Valley floor) there are only a little over 4 frost-free months (127 days), with the area near the town of Revelstoke (elevation 456 m) being somewhat warmer and drier (100-150 cm) than the rest of the park area. Much of the butterfly fauna resident in the Rocky Mountains (Banff and Jasper National Parks, Alberta) is missing from this area, probably due to the high precipitation and late spring combined with the lack of open habitats below treeline.

Data for this report were compiled from collections made in 1980, 1981 and 1983 and general observations from 1965 to 1979. All species reported were collected by the author under the authority of a Parks Canada volunteer agreement. The Biosystematics Research Institute, Ottawa, Ontario, Canada, confirmed the identification of all specimens to species level. A representative collection has been placed in the parks collection at Glacier Park nature center and selected specimens retained by the Biosystematics Research Institute. Specific collection data have been placed in the fauna files maintained by the park naturalists at Glacier Park nature center. Sixty-three species are confirmed for the parks. An additional eight are possible additions. A species list for the alpine areas of Mt. Cartier, Selkirk Range, and Mt. Begbie, Monashee Range (both 12-13 km south of Revelstoke) is given at the end. Mt. Begbie was collected 7 August 1983 and Mt. Cartier on 4 August 1983. These specimens are in the collection of John H. Shepard. Experience with the British Columbia butterfly fauna leads me to believe that the majority of the species regularly occurring in the parks are now documented.

The scientific names employed generally conform to those used in Howe (1975). The subspecies designation should be treated with caution because the taxonomic status of many species in this area is only poorly known.

For each species, the abundance, habitat, altitudinal range, flight period, and park(s) in which it is found are given. Five terms are used to describe abundance:

(1) Common: a species usually encountered every day in numbers,

(2) Uncommon: a species encountered on most days usually in small numbers,

(3) Rare: a species of which few are encountered, and encounters are infrequent during a year,

(4) Extremely rare: a species not seen most years with few records for any given location,

(5) Local: a species known only from restricted localities and habitats. May be common or rare depending upon the circumstances.

The descriptions of habitats and elevations are based on observation within the parks. Flight seasons are normally fairly constant, although during inclement weather emergence may be delayed by two or three weeks. There are a few species that appear to be found in only one of the

parks. Question marks indicate that certain species may occur in both parks, although thus far having been found only in one park.

Systematic Account

Hesperiidae (Latreille 1809)

1. **Thorybes pylades** (Scudder 1870): Abundance variable, rare to uncommon and local; forest edges, clearing, and roadsides up to 550 m; mid-May through June; M.R.N.P. only.
2. **Erynnis icelus** (Scudder and Burgess 1870): Common: open forest edges and roadside clearings; 456-914 m; May to early June; both parks.
3. **Pyrgus centaurae loki** (Evans 1953): Local and uncommon; dry alpine tundra and occasionally moist tundra; 2042-2134 m; July; both parks (Selkirk and Purcell Ranges). This species and *Hesperia comma* are found at higher elevations than any other Hesperiidae within the parks.
4. **Pyrgus ruralis** (Boisduval 1852): Rare to uncommon; dry grassy clearings, gravel road shoulders with short grass, and dry open areas where *Dryas* grows; 456-549 m; late April through June; M.R.N.P. only(?).
5. **Carterocephalus palaemon mandan** (W. H. Edwards 1863): Uncommon to common; wet grassy bogs close to forest edges; 457-1219 m; June and July; both parks.
6. **Thymelicus lineola** (Ochsenheimer 1808): Rare; open grassy areas such as fields and roadsides; one record for M.R.N.P. at 549 m in June. Appeared at Sicamous, B. C. 72 km west of Revelstoke several years ago and is rapidly spreading in all directions. The population within the parks is still expanding. The nearest collection site outside the parks was 15 km south of Revelstoke at 456 m in June 1981.
7. **Hesperia comma manitoba** (Scudder 1874): Rare and local; open subalpine forests, clearings, bogs and rockslides near timberline; 1859-2042 m; July and early August; both parks (Selkirk and Purcell Ranges).
8. **Polites themistocles** (Latreille 1824): Rare; grassy openings near forest edges and fields up to 610 m; June to early July; M.R.N.P. only.
9. **P. mystic** (W. H. Edwards 1863) ssp.: Rare; grassy openings near forest edges and fields up to 549 m; June and early July; M.R.N.P. only.
10. **Ochlodes sylvanoides** (Bosiduval 1852) ssp.: Very common; forest openings and edges, roadsides; up to 549 m; late July to mid-September; M.R.N.P. only.
11. **Amblyscirtes vialis** (Edwards 1862): Uncommon; clearings, forest edges, and along forest roads up to 762 m; late May to early July; M.R.N.P. only.

Papilionidae Latreille 1809

12. **Papilio zelicaon zelicaon** (W. H. Edwards 1852): Common to uncommon; forest edges, alpine meadows, mountain tops, riparian areas; 456-2438 m; mid-May to August; both parks.

13. **P. glaucus canadensis** (Rothschild and Jordan 1906): Common; forest edges, clearings, riparian areas, and open areas generally; p up to 1219 m; late May to mid-July.

14. **P. rutulus rutulus** (Lucus 1852): Extremely rare, three records for district; one record from G.N.P. (habitat, date, and elevation unknown), one record from Revelstoke (456 m) and one record in Rogers Pass (1300 m). The main blend zones for *P. rutulus* and *P. glaucus* are further west in the Okanagan-Shuswap Districts and south at the north end of Kootenay Lake.

15. **P. eurymedon** (Lucas 1852): Uncommon; riparian and open areas close to open forest edges and clearings, sometimes in association with *Ceanothus velutinus*; up to 640 m; late May to mid-July; M.R.N.P. only.

Pieridae Duponchel 1832

16. **Neophasia menapia tau** (?) (Scudder 1861): Uncommon; near forest edges; 518-2042 m; mid-July to mid-September; M.R.N.P. only(?).

17. **Pieris occidentalis occidentalis** (Reakirt 1866): Uncommon to common; roadsides, open forest edges, clearings, dry alpine tundra; 456-2438 m; late April to October; both parks (Selkirk and Purcell Ranges). At low elevations the early spring specimens are darker and sometimes smaller than summer specimens. At high elevations there is only the summer form present (mid-July to mid-August).

18. **P. napi** (Linnaeus 1758) ssp.: Common to uncommon; clearings in dense forest and forest edges along roadsides; 456-1859 m; late April to mid-August; both parks. At low elevations the summer brood is usually lighter than the spring brood. At high elevations only the darker form appears to be present.

19. **P. rapae** (Linnaeus 1758): Uncommon to common; widespread, but mostly near human habitations; 456-549 m; late April to early October, M.R.N.P. only (?).

20. **Anthocaris sara** Lucus 1852 ssp.: Common; open forest edges, roadsides, and clearings; 456-640 m; late April to early July; M.R.N.P. only (?).

21. **Colias philodice eriphyle** W. H. Edwards 1876: Common; open areas such as roadsides, clearings, forest edges, and dry areas of alpine meadows; 456-1829 m; late April to October; both parks.

22. **C. eurytheme** Boisduval 1852: Rare to uncommon; roadsides, fields, clearings, open forest edges; 456-762 m; mid-July to October; M.R.N.P. only. This species is probably a migrant to this area since it is not seen every year.

23. **C. nastes streckeri** Grum-Grischimailo 1985: Uncommon and local; barren mountain ridges and dry alpine tundra; probably mid-July to mid-August; one record for 2499 m on Dawn Mt., Purcell Range, G.N.P.

24. **C. pelidne minisni** Barnes 1895: Extremely rare; one record at 2438 m in G.N.P. on a ridge north of Dawn Mt. on the border of G.N.P. (could be a wind blown stray from lower down), 17 August 1981.

25. **Lycaena cupreus henryae** (Cadbury 1937): Rare and local; windswept barren ridges and rockslides; 2017-2134 m; mid-July to late August; G.N.P. on the ridges near Dawn Mt. (Purcell Range) and on Avalanche Crest (Selkirk Range).

26. **L. helloides** (Boisduval 1852): Common, local in G.N.P.; open areas such as roadside, forest edges, and fields; 459-909 m; mid-May to September; both parks. At least double-brooded at Revelstoke, probably single-brooded in most of the park areas.

27. **L. mariposa** Reakirt 1866 ssp.: Uncommon to common; forest clearings, edges of bogs, riparian areas, moist clearings near trails; 488-1463 m; late June to late August; both parks.

28. **Satyrium acadica colinensis** (Watson and W. P. Comstock 1920): Common; forest edges in association with *Salix* ssp., clearings, and riparian areas; 456-914 m; late June to early September; both parks. Material from this area is of uncertain affinity, but is closest to *acadica coolinensis* (J. H. Shepard, *in litt.*).

29. **Callophrys spinetorum** (Hewitson 1867): Extremely rare; one record at 946 m along a roadside (Trans-Canada Highway) forest edge in early July in G.N.P.

30. **C. rosneri rosneri** K. Johnson 1976: Rare to uncommon; damp roadsides close to forest edges; up to 457 m; mid-May to mid-June; M.R.N.P. only.

32. **C. augustus iroides** (Boisduval 1852): Common; roadsides close to forest edges and in clearings; 456-762 m; late April to early June; M.R.N.P. only.

32. **C. eryphon eryphon** (Boisduval 1852): Common; open forest edges close to roadsides; 456-914 m; late April to early June; both parks.

33. **Everes amyntula albrighti** Clench 1944: Uncommon to rare; open forest edges around clearings, sometimes attracted to damp spots along roadsides; 456-549 m; mid-May to mid-June; M.R.N.P. only.

34. **Celastrina argiolus nigrescens** (Flectcher 1903): Common; open forest edges, damp forest roads, clearings, and riparian areas; 456-945 m; mid-April to early July; both parks. This is the first species to appear in the spring in the parks, other than those which overwinter as adults. Eliot and Kawazoe (1983) consider *nigrescens* to be a hybrid population between spp. *lucia* and *echo*.

35. **Glaucopsyche lygdamus columbia** (Skinner 1917): Uncommon; clearings, avalanche paths, forest edges, mountain meadows; 456-1829 m; late April to mid-August; both parks.

36. **Lycaeides idas atrapraetextus** (Field 1939): Rare; along roadside gravel banks close to forest edges; 731-1311 m; late June to mid-August; M.R.N.P. only(?). The species name is *idas*, rather than *argyrognomon* (Berstrasser), as a consequence of I.C.Z.N. Opinion 269 and work by L. G. Higgins (C. D. Ferris, *in litt.*).

37. **Plebejus saepiolus amica** (W. H. Edwards 1863): Common; roadsides, open forest edges, bog edges, damp grassy meadows, fields; 456-1219 m; June to August; both parks.

38. **Agriades rustica megalo** W. H. Edwards 1927): Rare, occasionally locally common; rockslides, barren rocky ridges, open subalpine forest edges; 1981-2164 m; mid-July to early September; both parks (Selkirk and Purcell Ranges). *A. franklinii* is a low elevation, coastal arctic species with Leguminoseae foodplants. *A. rustica* is a montane species which feeds on *Saxifraga* (C. D. Ferris, *in litt.*).

Nymphalidae Swanison 1827

39. **Speyeria atlantis beani** (Barnes and Benjamin 1926): Common; mountain meadows, forest edges, bog edges, clearings; 456-1676 m; late June to early August; both parks. The commonest and most variable *Speyeria* in area.

40. **S. hydaspe sakuntala** (Skinner 1911): Uncommon to common; damp places along forest edges and riparian areas, mountain meadows and subalpine forest clearings; 456-1829 m; early July to September; both parks.

41. **S. mormonia opis** (W.H. Edwardes 1874): Uncommon; mountain meadows adjacent to open subalpine forests; 1219-1981 m; July to early September; both parks.

42. **Boloria selene atrocostalis** (Huard 1927): Uncommon and local; edges of wet grassy bogs and meadows; up to 917 m; late May to mid-August; G.N.P. only.

43. **B. epithore chermocki** (E. and S. Perkins 1966): Common; open forest edges, edges of bogs, clearings, riparian areas, mountain meadows; 456-1920 m; late May to mid-August; both parks.

44. **B. astarte astarte** (Doubleday and Hewitson 1847): Rare, local; barren windswept ridges and scree slopes; 2438-2621 m; mid-July to mid-August; Dawn Mt. summit (Purcell Range) and Avalanche Crest (Selkik Range) in G.N.P., Mt. Williamson (2045 m); in M.R.N.P.

45. **Phyciodes tharos** (Drury 1773) ssp.: Common; roadsides, fields, clearings, forest edges; 456-914 m; late May to early August; both parks. Subspecific status uncertain.

46. **P. campestris campestris** (Behr 1863): Uncommon; roadside clearings, open forest edges; 456-945 m; late May to early August; both parks.

47. **P. mylitta mylitta** (W.H. Edwards 1861): Extremely rare; dry roadsides near clearings, forest edges, open fields; 456-457 m; mid-May to late September; M.R.N.P. only. Also found 19 air km. south of Revelstoke in a field in the Akolkolex River area at 456 m (May 18, 1970). Possible two broods south of Revelstoke, and at least one brood in the park.

48. **Euphydryas anicia anicia** (Doubleday and Hewitson 1848): Common; mountain meadows, rockslides, subalpine forest edges, clearings, ridges; 1859-2073 m; late June to early September; both parks (Selkirk and Purcell Ranges).

49. **Polygonia satyrus** (W.H. Edwards 1869): Common; open forest, damp forest roads, forest edges, and riparian areas; 456-1219 m; in

flight late March to October, adult overwinters; both parks. Subspecies '*neomarsayas*', sometimes attributed to this area, is probably not a valid subspecies but simply a form (C.D. Ferris, *in litt.*).

50. **P. faunus rusticus** (W.H. Edwards 1874): Common; open forest, damp forest roads, forest edges, and riparian areas; 456-1829 m; in flight late March to October, adult overwinters; both parks.

51. **P. zephyrus** (W.H. Edwards 1870): Uncommon; open forest edges, mountain meadows, subalpine clearings; 456-1981 m; in flight late March to October, adult overwinters; both parks. Found at higher elevations and visits flowers (Compositae) more frequently than the other two *Polygonia* species in this area.

52. **Nymphalis vau-album watsoni** (Hall 1924): Uncommon at times; forest edges along damp roadsides; 456-945 m; in flight late March to October, adult overwinters; both parks. There are major population fluctuations every few years.

53. **N. californica herri** Field 1936: Rare; open forest edges, roadsides, clearings; 456-549 m; in flight late March to October; M.R.N.P. only(?). Migrates into area. Adult probably does not overwinter in the parks.

54. **N. antiopa antiopa** (Linneaus 1758): Common; riparian areas, forest edges, clearings, and damp forest roads; 456-1036; in flight late March to October, adult overwinters; both parks.

55. **N. milberti milberti** (Godart 1819): Common; mountain meadows, forest edges, riparian areas, clearings; 456-1981 m; in flight late March to October, adult overwinters; both parks.

56. **Vanessa cardui** (Linnaeus 1758): Common during some years; open sunny areas, clearings, meadows; 456-1524 m; May to October, adult does not overwinter, but instead migrates into the area some years; both parks.

57. **V. annabella** (Field 1971): Rare to uncommon in some years; roadsides close to forest edges; 456-1219 m; May to October, adult probably does not overwinter, but instead migrates in during some years; both parks. Not seen every year.

58. **Vaqnessa atalanta rubria** (Furhstorfer 1909): Rare to uncommon during some years; open forest edges, riparian areas, clearings, 456-1067 m; May to October, adult probably does not overwinter, but instead migrates in some years; both parks. Not seen every year.

59. **Limenitis lorquini burrisoni** (Maynard 1891): Common; riparian areas, damp forest roads, and forest edges; 456-1097 m; late-June to early August; both parks. Seldom seen visiting flowers but comes to moisture, manure, and mud.

Satyridae Boisduval 1833

60. **Cercyonis pegala boopis** (Behr 1864): Locally common; grassy clearings along forest edges; one locality at 549 m along the main trail to the summit of Mt. Revelstoke, mid-July to late August, M.R.N.P. only.

61. **Oeneis chryxus chryxus** (Doubleday and Hewitson 1849): Rare

and local; bases of rockslides close to grassy clearings, edges of subalpine forests and rocky alpine draws; 1524-1981 m; July to mid-August; G.N.P. (Selkirk and Purcell Ranges) only(?).

62. **Oeneis melissa beani** Elwes 1893; Rare and local; rocky screes and barren windswept short grass ridges; 2134-2438 m; late June to late July; G.N.P. (Selkirk and Purcell Ranges) only(?).

Danaidae Duponchel 1844

63. **Danaus plexippus** (Linnaeus 1758): An extremely rare migrant; one record at 457 m in August, 1973 on the south edge of M.R.N.P.; one record at Revelstoke in July 1957.

Possible additional species

There are a few additional species which might occur in the parks, either because they have been collected elsewhere in the Revelstoke District or because suitable habitats have not been completely sampled.

64. **Erynnis persius fredericki** H. A. Freeman 1943: This species could enter G.N.P. through the Beaver River valley. A mid-May to early July flight period would be expected.

65. **Polites coras** (Cramer 1775): Another species which could enter G.N.P. through the Beaver River valley. A mid-June to August flight period would be expected.

66. **Parnassius phoebus smintheus** Doubleday 1847: One specimen was taken 13 km south of Revelstoke in June 1980 at 456 m, and six specimens were taken on Mt. Cartier at 1615 m 4 August 1983. One female taken 37 km southeast of Revelstoke on the Akolkolex Forestry Road at elevation 677 m on 19 July 1983. Nomenclature follows that of Ferris (1976). This species may occur in the parks where its foodplant (*Sedum* spp.) grows in open rocky areas.

67. **P. multicaudatus** (W. F. Kirby 1884): A single specimen taken in the Akolkolex Valley 30 km southeast of Revelstoke in July 1970 at 640 m.

68. **Euptoieta claudia** (Cramer 1775): One specimen seen but not collected on Dawn Mtn., Purcell Range, G.N.P. at 2499 m 12 August 1981.

69. **Boloria euphrosyne** (Linnaeus 1758): Jones (1951) listed this species as occurring in the Revelstoke area. *B. euphrosyne* is not found in the Nearctic, his record is a mislabelled European specimen (J. H. Shepard, *in litt.*).

70. **Limenitis arthemis rubrofasciata** (Barnes and McDunnough 1916): One specimen collected 13 km south of Revelstoke at 456 m on June 23, 1982, near the junction of the Old South Highway and the Akolkolex Forestry Road. Currently in the collection of J. H. Shepard.

71. **Erbia epipsodea epipsodea** Butler 1868: Apparently absent from the parks, but might occur in G.N.P. in Grizzly Creek area at 1890-2075 m.

72. **Oeneis jutta chermocki** Wyatt 1965: Suitable habitat is present in the Beaver River Valley in G.N.P. at 945-1219 m. A likely flight period would be late June to mide-July. May be biennial and missed on the off years.

Alpine species found on Mt. Begbie and Mt Cartier

1. **Pyrgus centaurae loki** (Evans 1953): 2316 m on Mt. Begbie. This species and *L. cupreus* may also occur on Mt. Cartier.
2. **Hesperia comma manitoba** (Scudder 1874): 2316 m on mt. Cartier.
3. **Pieris occidentalis occidentalis** (Reakirt 1866): 2286-2408 m on Mt. Begbie; 2469 m on Mt. Cartier.
4. **Colias nastes streckeri** (Grum-Grischimailo 1895): 2194 m on Mt. Begbie; 2347 m on Mt. Cartier.
5. **Lycaena cupreus henryae** (Cadbury 1937): 2225 m on Mt. Begbie.
6. **Agriades rustica megalo** (W. H. Edwards 1927): 2225-2732 m on Mt. Begbie; 1615-2316 m on Mt. Cartier.
7. **Boloria astarte astarte** (Doubleday and Hewitson 1847): 2225-2732 m on Mt. Begbie; 2408-2610 m on Mt. Cartier.
8. **Euphydryas anicia anicia** (Doubleday and Hewitson 1848): 2316 m on Mt. Begbie; 1646-2286 m on Mt. Cartier.
9. **Oeneis chryxus chryxus** (Doubleday and Hewitson 1849): 2316 m on Mt. Begbie; 2225-2316 m on Mt. Cartier.
10. **Oeneis melisa beani** Elwes 1893: 2732 m on Mt. Begfbie; 2469 m on Mt. Cartier.

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Hybridization of the Mexican tiger swallowtail, *Papilio alexiares garcia* (Lepidoptera: Papilionidae) with other *P. glaucus* group species and survival of pure and hybrid larvae on potential host plants

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Abstract. Mexican tiger swallowtails, *Papilio alexiares garcia* were collected in Nuevo Leon and Tamaulipas. Males and virgin females were hybridized with other *P. glaucus* group species. Crosses with *P. glaucus* had normal egg viability and a 1:1 sex ratio of hybrid adults. Fewer crosses with other species and subspecies were made, and the results were more variable. Inheritance of the dark female morph appeared to be the same in *P. a. garcia* as in *P. glaucus*. Pure *P. a. garcia* neonate larvae survived best on *Prunus serotina*, the natural host, and on other Rosaceae and Oleaceae with intermediate survival on species of Rutaceae, Magnoliaceae, Platanaceae, and Betulaceae. Salicaceae and Rhamnaceae species were of little value as larval hosts. In general, hybrid survival was similar but showed influences of the *P. glaucus* subspecies that was the female parent.

Introduction

Two Mexican tiger swallowtail butterfly subspecies have been described (*Papilio alexiares alexiares* Hopffer and *P. a. garcia* Rothschild and Jordan), but little is known about their biology (Brower, 1958; Scriber, 1973; Frances & Elvira, 1978; Beutelspacher & Howe, 1984). The subspecies *P. a. alexiares* ranges throughout the states of Hidalgo, Puebla, and Veracruz, northeast of Mexico City at altitudes from 500 m to 2600 m. Both sexes are the yellow tiger-striped morph (Beutelspacher & Howe, 1984; Tyler, 1975; Jorge Llorente Bosquets, pers. comm.). *P. a. garcia* is found further to the north in Tamaulipas, Nuevo Leon, and San Luis Potosi (Fig. 1) and is reported to have only dark morph females (Beutelspacher & Howe, 1984; Lee D. Miller, pers. comm.). On the basis of male genitalia, Brower (1959) suggested that *P. alexiares* was more

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closely allied to the western species (*P. rutulus* Lucas, *P. eurymedon* Lucas, and *P. multicaudatus* Kirby) than to *P. glaucus*. L. Genetic distance data derived from allozyme electrophoresis in our laboratory support this contention (Hagen and Scriber, in prep.)

Recently, black cherry (*Prunus serotina* Ehrh.) has been observed to be one of the natural hosts of *P. a. garcia* (Evans et al., 1988; Fig 2). In this paper, we report larval acceptance and survival on various potential foodplant species used elsewhere in North America by the *Papilio glaucus* and/or *troilus* species groups. We also present data detailing various interspecific hand-pairings of *P. a. garcia* with other *Papilio glaucus* species group members. These data provide additional insights into the genetics of the dark morph female color polymorphism in the *Papilio glaucus* species group (see Clarke & Sheppard, 1959; 1962; Scriber, 1985; Scriber et al., 1986; Scriber & Evans, 1987 for discussion).

Methods

Both male and female *P. a. garcia* were collected in Nuevo Leon and Tamaulipas, Mexico in March and April, June, and August and September 1984, 1986 and 1987. Enveloped specimens were either mailed or carried on ice to our laboratory.

Male *P. a. garcia* were hand-paired to virgin *P. a. garcia* females or virgin females of other *Papilio glaucus* group species. Field-collected and laboratory-mated females were set up in plastic boxes (10 cm × 20 cm × 27 cm) with a sprig of black cherry, *Prunus serotina*, under saturated humidity. The boxes were placed 0.7-1.0 m from continuously lighted 100 watt incandescent bulbs. Females were fed a mixture of 1 part honey to 4 parts water at least once daily. Most females were allowed to oviposit until death. After they died, hand-paired females were dissected, and the presence of spermatophores was determined. Any female not containing a spermatophore was eliminated from analysis. Field-collected females were not routinely dissected for this study because virgin *Papilio* females are rarely collected (Burns, 1968; Makielski, 1972; Pliske, 1972; Platt et al., 1984; Lederhouse & Scriber 1987a).

Eggs were collected and counted at 2-day intervals except on weekends. Larvae were removed as they hatched, and the remaining eggs were monitored for 10 days after the last larva hatched. Egg viability was the proportion of the total eggs laid that hatched as larvae. Using fine camel-hair brushes, first instar larvae (neonate) were gently placed on fresh leaves of various potential hostplants for bioassays of consumption and survival. Leaf moisture was maintained using aquapics, and fresh leaves were provided 3 times per week throughout larval development. Larval survival equaled the percent of first instars set up on a host that successfully molted to the second instar. Means were calculated with each mother considered a replicate. Some progeny of field-collected *P. a. garcia* females were used in subsequent matings.

Results and Discussion

The pattern of oviposition of 26 field-collected and 36 hand-paired *P. a. garcia* was similar to that of the 3 *P. glaucus* subspecies (Table 1). In

general somewhat more than half of the females that were set up laid some eggs. Of those females than laid eggs, field-collected females were more likely that hand-paired females to produce larvae from their clutches (X^2, $p < 0.01$ in each case). The mean viability of *P. a. garcia* clutches laid by field-collected females was similar to those of comparable females of each *P. glaucus* subspecies (Lederhouse & Scriber, 1987a). There was considerable clutch to clutch variability in larval hatching.

Spermatophores were passed during hand-pairings between *P. a. garcia* males and females and other *P. glaucus* group species (Table 2).

Table 1. Oviposition characteristics of field-collected and laboratory reared and hand-mated females of *Papilio alexiares garcia* and *P. glaucus* subspecies. A subsample of females that had laid more than 10 eggs was used to calculate mean egg viability.

Phenotype	No. females	% laying eggs	% layers with larvae	n	Egg Viability (%) mean	range
P. alexiares						
field	26	65.4	76.5	11	51.3	10.6–80.9
hand-paired	36	58.3	28.6	5	34.6	4.5–73.3
P. g. glaucus						
field	959	54.6	70.4	63	59.3	1.6–100.0
hand-paired	191	87.4	26.3	35	52.7	8.3–100.0
P. g. canadensis						
field	730	48.4	65.2	50	55.9	2.4–95.0
hand-paired	69	82.6	19.3	9	29.7	2.4–95.5
P. g. australis						
field	85	70.6	73.3	31	58.7	0.7–97.1
hand-paired	0	–	–	–	–	–

Fig. 1. Typical habitat of *Papilio alexiares garcia* west of Cola de Caballo, Nuevo Leon, Mexico at an elevation of about 1000 m.

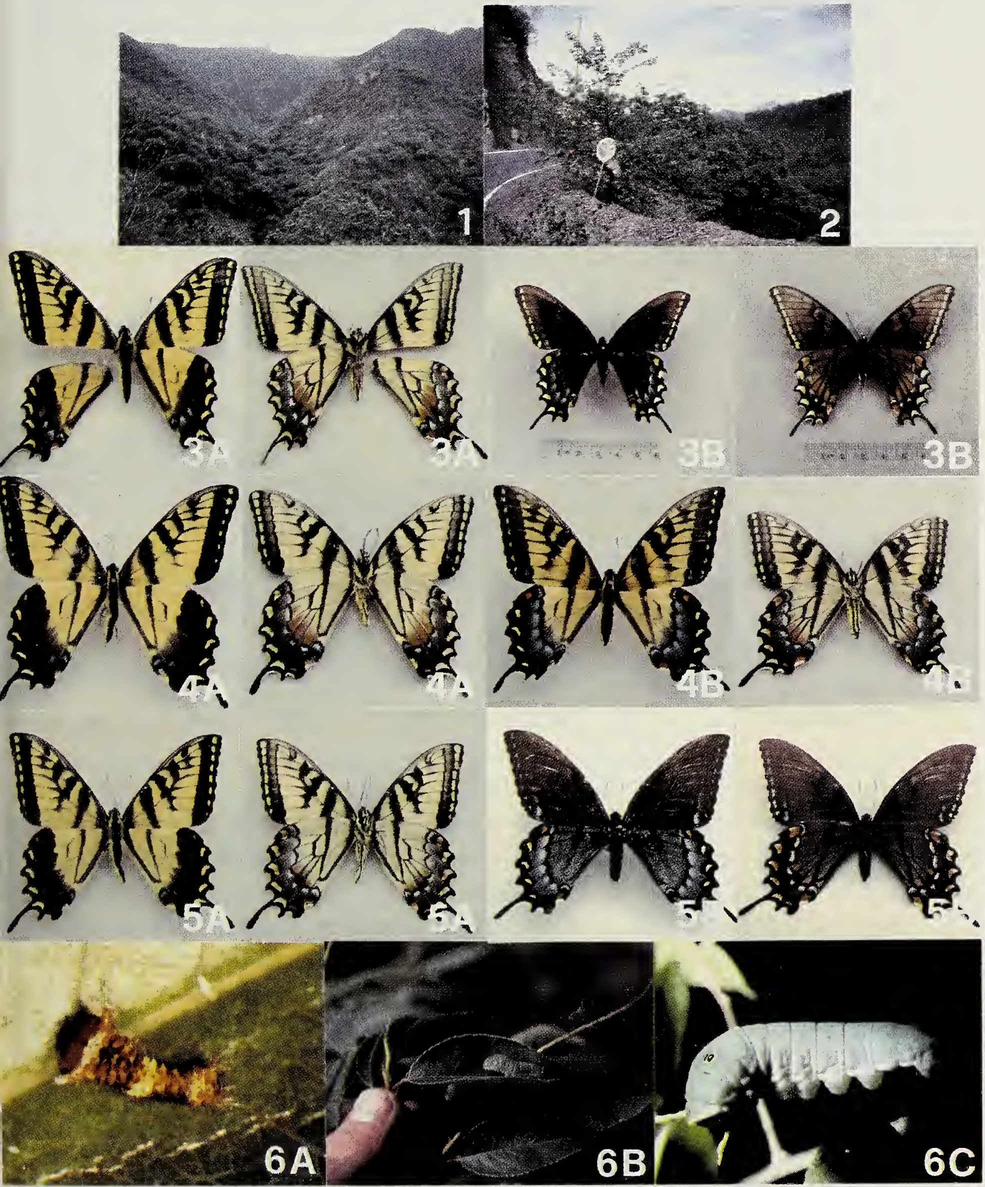
Fig. 2. Black cherry tree (*Prunus serotina*) where *P. a. garcia* larvae were collected. The tree was at about 1100 m elevation on Chipinque Mesa, Nuevo Leon, Mexico.

Fig. 3. Adult *P. a. garcia* collected in Nuevo Leon, Mexico. A. Male dorsal and ventral, 15 April 1984. B. Female dorsal and ventral, 23 March 1985.

Fig. 4. Representative hybrid adults from a yellow Ohio *P. g. glaucus* female and a *P. a. garcia* male (pairing 1071). A. Male dorsal and ventral. B. Female dorsal and ventral.

Fig. 5. Representative hybrid adults from a dark Ohio *P. g. glaucus* female and the same *P. a. garcia* male (pairing 1100). A. Male dorsal and ventral. B. Female dorsal and ventral.

Fig. 6. Larvae of *P. a. garcia* reared on black cherry. A. Neonate. B. Larva molting into the final instar found on black cherry in the field. C. Final (fifth) instar.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2
3A
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5A
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6B
6C

Table 2. Oviposition characteristics of *P. glaucus* species-group females hand-paired with *Papilio alexiares garcia* males and *P. a. garcia* females hand-paired with *P. glaucus* species-group males. The female parent is listed first. Mean and range of viabilities of hybrid eggs are presented. All females were dissected, and only those containing a spermatophore are considered. Mean number of eggs and percent egg viability is presented only for females with at least one larvae.

Phenotype	Mated females	% laying eggs	% layers with larvae	Egg Mean	Egg Viability (%) Mean	Egg Viability (%) Range
P. g. glaucus x *P. alexiares*	24	87.5	76.2	173.9	66.1	28.4–96.9
P. g. canadensis x *P. alexiares*	7	100.0	71.4	71.0	35.7	2.1–67.9
P. g. australis x *P. alexiares*	6	83.3	100.0	105.8	34.8	11.5–59.1
P. rutulus x *P. alexiares*	1	100.0	0.0	–	–	–
P. alexiares x *P. g. glaucus*	3	100.0	33.3	15.0	60.0	–
P. alexiares x *P. g. canadensis*	1	100.0	100.0	1.0	100.0	–
P. alexiares x *P. g. australis*	1	100.0	100.0	21.0	9.5	–
P. alexiares x *P. rutulus*	1	100.0	100.0	113.0	33.6	–
P. alexiares x *P. eurymedon*	1	100.0	0.0	–	–	–

Nearly all females laid eggs. The mean viability of eggs from female *P. g. glaucus* and *P. a. garcia* males was equivalent to that of field-collected pure subspecies (Table 1). Egg viability of other hybrid crosses was lower, but not lower than that of hand-paired pure subspecies. Sex ratios at adult emergence totaled 240 males to 211 females for *P. g. glaucus* females × *P. a. garcia* males, 37:32 for *P. g. australis* females × *P. a. garcia* males, and 8:10 for *P. g. canadensis* females × *P. a. garcia* males (Table 3). None of these ratios differs significantly from an expected of 1:1 (X^2, $p > 0.20$ in each case). These results are further evidence of high genetic compatibility between *P. glaucus* and *P. a. garcia*.

The crosses between male *P. a. garcia* and female *P. g. glaucus* or *P. g. australis* were particularly interesting since these are the only members of the entire North American tiger swallowtail group that have dark female polymorphism (Fig. 3; Clarke & Sheppard, 1962; Scriber et al., 1987; Lederhouse & Scriber, 1987b). Our data (Table 3)

Table 3. Hybrid pairings of the two color morphs of *P. glaucus* subspecies females with *P. alexiares garcia* males and the resulting offspring. *Papilio glaucus* females were reared from mothers collected in Ohio, Illinois, Wisconsin and Florida.

Mating number	Phenotypes	Dead pupae	Males	Yellow females	Dark females
P. g. glaucus					
1071	Yellow OH x male 1	7	58	42	1
1072	Yellow OH x male 2	3	8	8	0
1100	Dark OH x male 1	14	61	1	49
4210	Dark OH x male 3	3	32	2	27
4211	Dark IL x male 4	7	47	2	52
4227	Dark OH x male 5	0	5	0	2
4228	Dark IL x male 6	0	5	0	5
4230	Dark IL x male 3	0	8	2	9
4234	Dark OH x male 7	0	3	0	7
4458	Dark OH x male 8	0	5	0	1
4471	Yellow OH x male 9	0	8	1	0
P. g. australis					
3547	Dark FL x male 10	0	27	0	27
4581	Yellow FL x male 11	1	8	3	0
4587	Yellow FL x male 12	0	1	1	0
4598	Yellow FL x male 13	0	1	1	0
P. g. canadensis					
1625	Yellow WI x male 14	0	0	2	0
3368	Yellow WI x male 15	0	0	1	0
4457	Yellow WI x male 16	0	2	5	0
4470	Yellow WI x male 17	1	6	2	0

suggest that the same genetic basis is likely to be involved for all 3 taxa: a Y-linked gene for melanism without color suppressors in males (Scriber, 1985; Scriber et al., 1987). Dark females (XY^D) generally produce dark daughters regardless of the color of the mother of their mate, and yellow females (XY) generally only produce yellow daughters (Table 3). Occasionally, a female offspring of the opposite color from her mother will be produced (Hagen & Scriber, 1989). Possible explanations of such results are discussed elsewhere (Clarke at al. 1976, Scriber et al. 1987). Hybrid pairings of the same *P. a. garcia* male with a yellow female and a dark female produced daughters of the expected phenotype (pairing 1071, Fig. 4, pairing 1100, Fig. 5). The same pattern held for *P. g. australis* females crossed with *P. a. garcia* males (Table 3). All hybrid females from *P. g. canadensis* females crossed with *P. a. garcia* males were yellow (Table 3); *P. g. canadensis* females lack the dark gene (Scriber et al. 1987).

The newly eclosed first instar larvae of *P. a. garcia* and *P. glaucus* subspecies hybrids with *P. a garcia* males exhibited differential survival in no-choice tests on leaves of 27 plant species from 10 plant families (Table 4). For pure *P. a garcia*, neonates survived best on black cherry (*Prunus serotina* Ehrh.), its natural host, other *Prunus* species,

Table 4. No-choice feeding bioassays of Mexican *Papilio alexiares garcia* and its hybrids. The female parent of hybrid larvae is listed first. The top value for survival is the mean percent; the lower value is the standard deviation.

Plant Family	Genus Species (common name)	*P. a. garcia* # of Fertile Females	# of Larvae	First Instar Survival	*P. g. glaucus* x *P. a. garcia* # of Fertile Females	# of Larvae	First Instar Survival	*P. g. australis* x *P. a. garcia* # of Fertile Females	# of Larvae	First Instar Survival	*P. g. canadensis* x *P. a. garcia* # of Fertile Females	# of Larvae	First Instar Survival
Rosaceae	*Prunus serotina* Ehrh. (Black Cherry)	17	299/337	76.4 37.2	13	558/679	82.9 10.6	4	40/49	82.9 23.6	4	29/46	67.5 26.2
Rosaceae	*Purnus virginiana* L. (Choke Cherry)	1	2/2	100.0 –	1	77/92	83.7 –	1	1/1	100.0 –	–		
Rosaceae	*Prunus angustifolia* Marsh (Chickasaw Plum)	5	14/23	59.4 17.0	–			–			–		
Oleaceae	*Fraxinus americana* L. (White Ash)	2	3/3	100.0 0.0	1	4/4	100.0	–			–		
Oleaceae	*Fraxinus pennsylvanica* Marsh (Green Ash)	–			3	3/25	29.4	–			–		
Oleaceae	*Ligustrum spp.* (Privet)	5	0/20	0.0 0.0	–			–			–		
Rutaceae	*Ptelea trifoliata*. L. (Hop Tree)	3	5/8	44.4 50.9	4	18/29	63.9 22.0	1	3/4	75.0 –	–		
Rutaceae	*Citrus spp.* (Grapefruit)	8	0/30	0.0 0.0	–			–			–		
Platanaceae	*Platanus occidentalis* L. (Sycamore)	3	3/6	38.9 34.7	2	2/40	4.8 6.7	1	2/2	100.0 –	–		
Betulaceae	*Betula papyrifera* Marsh. (Paper Birch)	2	2/5	41.7 11.8	–			–			–		
Salicaceae	*Salix caroliniana* Michx. (Coastalplain willow)	6	1/20	1.7 4.1	–			–			–		

Salicaceae	*Salix lasiolepis* Benth. (Arroyo willow)	–			3	4/30	11.1 19.2	–			1	7/14	50.0 –
Salicaceae	*Populus deltoides* Marsh. (Cottonwood)	1	0/1	0.0 –	1	0/5	0.0 –	1	0/2	0.0 –	–		
Salicaceae	*Populus grandidentata* Michx. (Big-toothed Aspen)	2	1/5	25.0 35.4	2	8/97	8.3 11.8	1	0/2	0.0 –	–		
Salicaceae	*Populus balsamifera* L. (Balsam Poplar)	2	0/3	0.0 0.0	–			1	2/2	100.0			
Salicaceae	*Populus tremuloides* (Michx.) (Quaking Aspen)	2	0/6	0.0 0.0	4	0/145	0.0 0.0	1	1/2	50.0 –	2	14/24	57.8 3.1
Rhamnaceae	*Rhamnus cathartica* L. (Buck thorn)	1	0/2	0.0	–			1	0/2	0.0	–		
Rhamnaceae	*Rhamnus californica* Eschsch. (Coffeeberry)	–			2	0/30	0.0 0.0	–			–		
Corylaceae	*Carpinus carolinana* Walt. (Hornbeam)	2	0/3	0.0 0.0	–			–			–		
Lauraceae	*Sassafras albidum (Nutt.)* (Sassafras)	–			2	7/9	80.0 28.3	–			–		
Lauraceae	*Lindera benzoin* (L.) Blume (Spicebush)	2	1/5	12.5 17.7	2	2/15	25.0 35.4	–			–		
Lauraceae	*Persea borbonia* (L.) Spreng. (Redbay)	4	0/16	0.0 0.0	3	0/76	0.0 0.0	–			–		
Lauraceae	*Myrica cerifera* L. (Wax myrtle)	4	0/8	0.0 0.0	–			–			–		
Lauraceae	*Cinnamomum camphora* L. (Camphor)	–			2	25/42	41.7 58.9	–			–		
Magnoliaceae	*Liriodendron tulipifera* L. (Tulip Tree)	3	3/7	44.4 50.9	2	63/74	83.9 5.5	4	14/14	100.0 0.0	–		
Magnoliaceae	*Magnolia virginiana* L. (Sweetbay)	9	5/46	4.3 12.8	4	57/96	51.9 35.7	3	4/11	58.3 52.0	–		
Magnoliaceae	*Magnolia acuminata* L. (Mountain Magnolia)	1	0/2	0.0 –	–			2	7/7	100.0 0.0	–		

and white ash (*Fraxinus americana* L.). Intermediate levels of survival were shown by *P. a. garcia* neonates on hoptree (*Ptelea trifoliata* L., Rutaceae), tuliptree (*Liriodendron tulipifera* L., Magnoliaceae), sycamore (*Platanus occidentalis* L., Platanaceae), and paper birch (*Betula papyrifera* Marsh., Betulaceae). Although sample sizes are small in some cases, plant species in the Salicaceae and Rhamnaceae are of minimal usefulness as food plants for the Mexican tiger swallowtail. First and final instar *P. a. garcia* larvae are shown in Figure 6.

In general, hybrid survival was similar to that of pure *P. a. garcia*, but showed the influence of the particular subspecies of *P. glaucus* that was the female parent (Table 4). Hybrid survival was uniformly high on black cherry, choke cherry (*Prunus virginiana* L.), and white ash. Hybrids from *P. g. glaucus* and *P. g. australis* mothers exhibited higher survival on hosts in the families Rutaceae, Lauraceae, and Magnoliaceae. Hybrids from *P. g. canadensis* mothers had enhanced survivorship on Salicaceae hosts (Table 4).

The Magnoliaceae and Salicaceae are believed to represent major adaptive radiations in host use for North American *Papilio* from a possible Lauraceae or Rutaceae root (Scriber, 1983; 1986). Larvae of *P. g. glaucus* and *P. g. australis* readily grow on Magnoliaceae but mostly die on Salicaceae; *P. g. canadensis, P. rutulus*, and *P. eurymedon* larvae exhibit the opposite abilities (Lindroth et al., 1986, 1988; Scriber et al., 1986). Should *P. alexiares* represent the ancestral stock (from southwestern Pleistocene refugia) for a *P. glaucus* species group radiation, we are not surprised that *P. alexiares* larvae possess some capabilities to detoxify and process foodplants from all 4 plant families. We continue to expand our studies to assess the degree of phylogenetic affiliation of *P. alexiares garcia* with other *P. glaucus* group taxa.

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The Butterflies of Isla de Cedros, Baja California Norte, Mexico

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Abstract. Isla de Cedros is an arid Pacific island off the western coast of Baja California Norte, Mexico. The island supports a depauperate butterfly fauna consistent with other offshore islands which exhibit varying degrees of faunal reduction when compared to their mainland counterparts. The 23 butterfly species recorded from Isla de Cedros reflect 2 broad categories of presumptive biogeographic origin: 1) species of Neotropical origin, which are distributed throughout the peninsula; and 2) species of Nearctic origin, some of which occur throughout the peninsula, and others confined to the Californian province of the adjacent peninsula. The 80 year history of entomological activity on the island is outlined; the physiography of the area is briefly discussed; and the 23 butterfly species are listed with capture records and taxonomic comments. Additionally, an endemic species, *Mitoura cedrosensis* is described and illustrated.

Introduction

The butterfly fauna of Isla de Cedros, Baja California Norte, Mexico, has been sampled on numerous occasions over the past 80 years, most recently by the authors in 1981 and 1983. A total of 23 butterfly species has been recorded from the island, including 1 endemic species and 1 endemic subspecies. This number is considerably less than the number of species that would be found in comparable habitats on the adjacent mainland. This fact is consistent with other offshore islands which exhibit varying degrees of faunal reduction, generally dependent upon their size and distance from continental masses (MacArthur and Wilson, 1967; Pielou, 1979; Langston, 1980). Geologic evidence of a previous landbridge to the peninsula of Baja California suggests the past opportunity for the development of a more diverse fauna than is currently evident. Pielou (1979) suggests that upon separation from the mainland, continental islands have an over-saturated biota, and that a period of floral and faunal reduction ensues until the number of species on the island falls to an appropriate equilibrium level. Clear evidence of faunal reduction has been given by Wilcox (1978) for the lizard faunas of several Baja California islands. In the butterfly fauna of Cedros,

however, the island appears to be in an under-saturated (non-equilibrium) condition.

The peninsula of Baja California can be divided into 3 major biotic provinces: a northwestern Californian region, a central desert region, and a southern subtropical thorn scrub region which includes the cape. Floral characteristics of the northwestern province occur as disjuncts southward on scattered higher peaks forming outposts of this region as far south as the mountains of the cape. Such an outpost occurs in the higher elevations of Isla de Cedros. Before the origin of the deserts in the late Quaternary, these southern relicts were presumably more nearly continuous with the northwestern region (Gould and Moran, 1981). As a consequence of this outpost effect, serveral Californian elements reach their southern limit on Isla de Cedros, considerably disjunct and isolated from the southern end of their contiguous peninsular populations to the north.

Collecting History

Although seldom a primary destination, Isla de Cedros has historically provided a stop-over for boat expeditions traveling along the Pacific coast of Baja California. The following outline briefly summarizes the historical accounts of entomological activity on the island.

1905. California Academy of Sciences Expedition to the Galapagos Islands. On Cedros 18 July 1905. F.X. Williams, entomologist.

1922. California Academy of Sciences Expedition to the Eastern Pacific Islands. On Cedros 22 July 1922. G. Hanna and J. Slevin, collectors.

1925. California Academy of Sciences Expediton to Revillagigedo Islands. On Cedros 2-6 June 1925. H. H. Keifer, entomologist.

1932. Allan Hancock Pacific Expedition. On Cedros 25 February 1932. J. S. Garth, entomologist.

1934. Allan Hancock Pacific Expedition. On Cedros 10 March 1934. J. S. Garth, entomologist.

1937. Allan Hancock Pacific Expedition. On Cedros 10 and 12 July 1937. J. S. Garth, entomologist.

1937-1939. Several boat trips to Baja California by F. Rindge family. F. H. Rindge, entomologist.

1941. Allan Hancock Pacific Expedition. On Cedros 28 February 1941. J. S. Garth, entomologist.

1949. Velero IV Gulf of California Cruise. On Cedros 4-5 March 1949. J. S. Garth, entomologist.

1981. San Diego Natural History Museum Expedition to Northern Baja California. On Cedros 20-23 March 1981. D. Faulkner and F. Andrews, entomologists.

1983. San Diego Natural History Museum Expedition to Isla de Cedros. On Cedros 28 March-5 April 1983. J. Brown and D. Faulkner, entomologists.

1983. Diamaresa Expedition to Pacific Islands Adjacent to Baja California. On Cedros 30 June-2 July 1983, 13 July 1983. D. Faulkner, D. Weissman, D. Lightfoot, and V. Lee, entomologists.

Although there have been a number of visits to the island in the past 80 years, few of the expeditions spent more than a brief time on the island, making only short trips into the more accessible localities, such as Cañon de la Mina in the north. This is reflected in the few Lepidoptera specimens available for examination as well as the low number of species recorded until recently.

Physiography

Geology. Isla de Cedros is a rather large (348 km^2), rugged, mountainous island (Fig. 1) situated about midway down the western side of the peninsula of Baja California, Mexico (Fig. 2). Oriented north to south, the island is about 34 km in length and varies from about 4 to 15 km in width. The southeastern extremity, Punta Morro Redondo, is separated from the mainland by a narrow and shallow strait 22 km wide. Projecting northwest from the mainland, Punta San Eugenio represents the southern connection of a presumed landbridge that once united Cedros with the peninsula (Gentry, 1950). It is likely that migrant species regularly reach Cedros by "island hopping" from Punta San Eugenio to Isla Natividad, and from there to Cedros.

The island's montane spine is bisected into a northern and a southern range by a deep gorge called El Gran Cañon or El Arroyo Grande. The highest point, Cerro de Cedros, in the southern half of the island,

Fig. 1. Eastern coast of Isla de Cedros, looking south from Punta Norte.

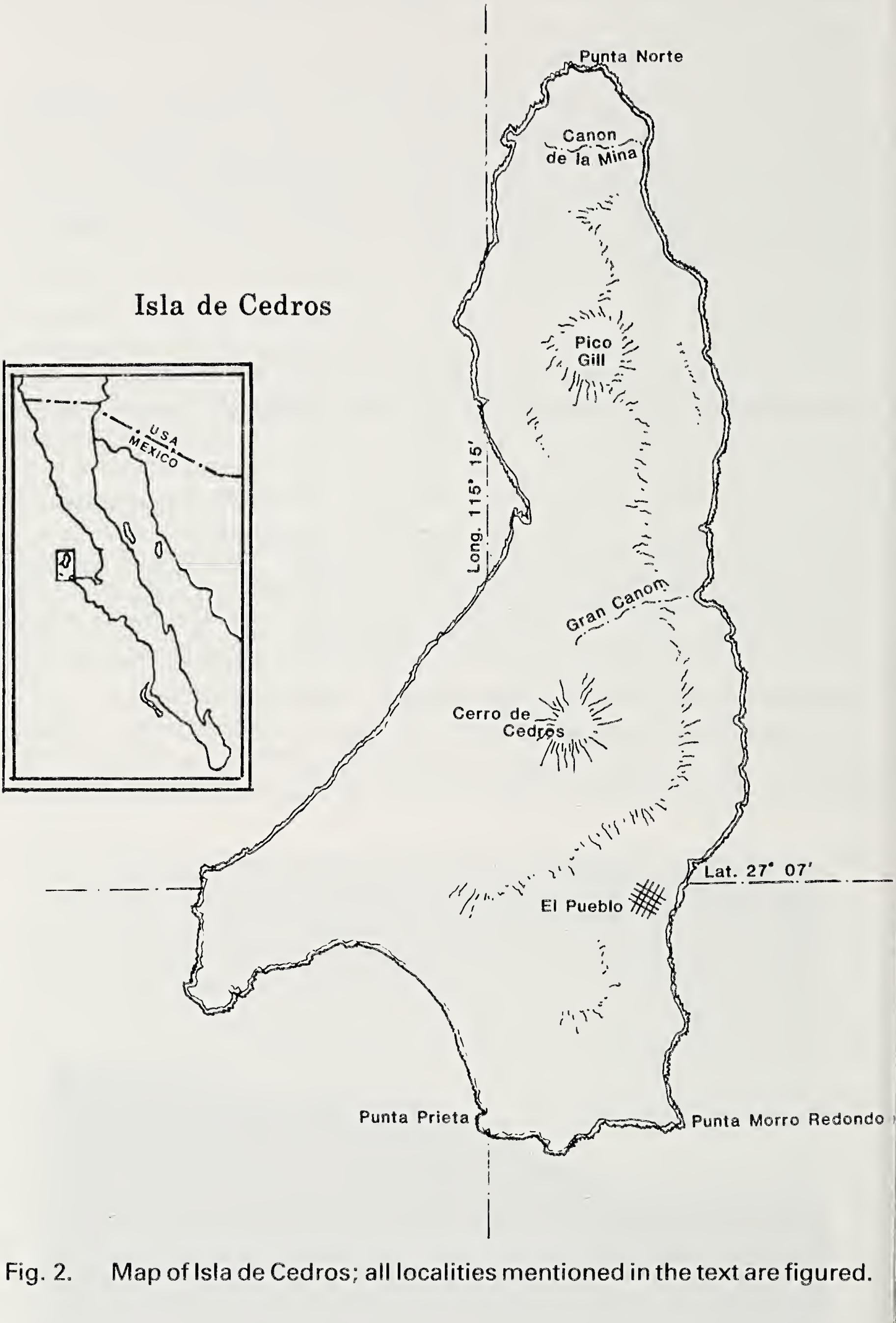


Fig. 2. Map of Isla de Cedros; all localities mentioned in the text are figured.

reaches an elevation of 1200 m (3950'). The uplifted sedimentary strata reflect a history of tremendous geologic disturbances. The granodioritic rocks present are of pre-Cretaceous and Pliocene origin (Wiggins, 1980).

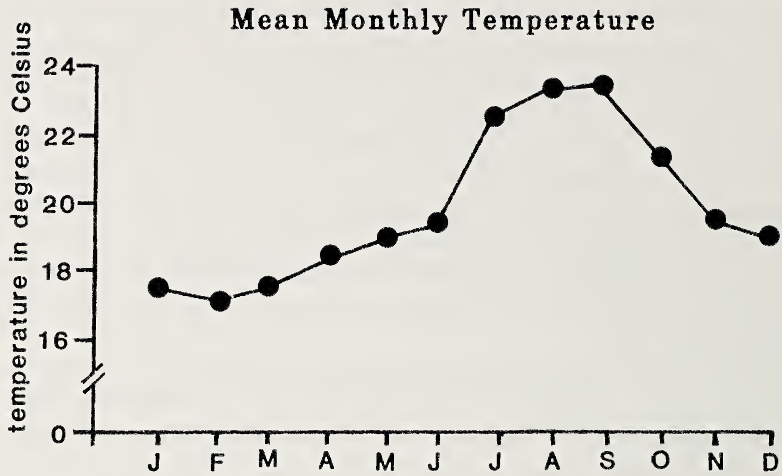
A reconnaissance of the geology of Isla de Cedros (Kilmer, 1977) indicates that the island was formed by an uplift of late Jurassic metamorphic and igneous rock at a point where the Pacific plate was subducted beneath the western margin of the North American plate. The possible geological relationship of Isla de Cedros with the California Channel Islands emphasizes the relationship between the small but striking relictual floral elements common to the two areas (Moran and Benedict, 1981).

Climate. The climate of Isla de Cedros is generally temperate owing to its proximity to Mediterranean climatic regimes; however, long, hot, dry spells are common. Cedros is near the southern edge of California's winter Pacific storm tract, and at the northern extreme of southern Baja California's tropical summer storm pattern. Precipition records, as a result, indicate extreme inconsistency in both seasons; in some years little or no rain reaches the island. Figure 3 provides climatological data adapted from Hastings and Humphrey (1969).

In the vicinity of Isla de Cedros, generally to the north and west, there are often low, dense mists or fog banks which are common in all seasons but particularly in the summer months (Libby, Bannister, and Linhart, 1968; Lewis and Ebeling, 1971). The abundant moisture provided by this condition has great influence in producing the luxuriant desert vegetation which occurs during certain seasons on parts of the western slopes (Nelson, 1921), and sustains the stands of Monterey pine that occur on the west and northwest escarpments of the island's northern range.

Flora

Because of its accessibility by ship, and more recently be cargo plane, the flora of Isla de Cedros has been rather extensively studied (Moran, 1972). Hale (1941) estimates that 97% of the island is covered by desert scrub vegetation similar to that occurring throughout the Vizcaino-Magdalena region of the adjacent peninsula. The most striking and conspicuous plants occurring over most of the island are the elephant tree (*Pachycormus discolor* (Benth.) Cov.) and the mescál (*Agave sebastiana* (Greene) Gentry) (Fig. 4). In small isolated areas the desert scrub gives way to other types of vegetation, most notably coastal sage scrub, chaparral, and even coniferous forest. The most remarkable departure from the desert vegetation is the closed-cone pine forests dominated by *Pinus radiata* var. *cedrosensis* J. T. Howell which occur in 2 major populations in the mountains (Libby, Bannister, and Linhart, 1968). Several Californian floral elements reach their southern limit on



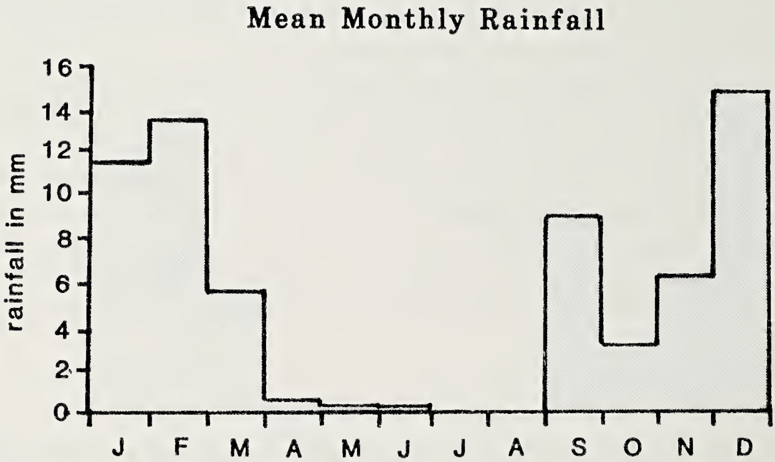


Fig. 3. Climatological data adapted from Hastings and Humphrey (1969). **Above**: Annual precipitation (in mm). **Below**: Average annual temperature (in °C).

Cedros including California juniper (*Juniperus californica* Carr.), lemonade berry (*Rhus integrifolia* (Nutt.) Rothr.), chamise (*Adenostoma fasciculatum* var. *obtusidolium* S. Wats.), and California sage brush (*Artemisia californica* Less.). The flora of the island includes 245 vascular plants, of which 216 species are native and 29 species introduced (Moran and Benedict, 1981). Of the native flora, 16 species are endemic to Isla de Cedros and are discussed by Moran (1972).

Butterfly Fauna

The 23 butterfly species recorded from Isla de Cedros represent 6 families: Hesperiidae (2 species), Pieridae (7 species), Lycaenidae (9

Fig. 4. **Above:** Fog-enshrouded Canon de la Mina at the north end of the island. The tall, white-flowered, endemic *Eriogonum molle* is conspicuously abundant. **Below**: Characteristic vegetation near the light-house at Punta Norte, dominated by *Agave sebastiana* and *Opuntia* species.

species), Riodinidae (2 species), Nymphalidae (2 species), and Danaidae (1 species). The 23 species reflect 2 extremely broad categories of biogeographic origin: the Neotropical and the Nearctic.

Species of Neotropical origin represented in the island's fauna are widespread forms that occur the entire length of the peninsula, extending more or less from South or Central America northward into southern California. Species in this category include *Erynnis funeralis, Phoebis sennae, Eurema nicippe, Strymon columella, Brephidium exilis, Leptotes marina, Hemiargus ceraunus,* and *Danaus gilippus.* These species represent approximately 35% of the total butterfly fauna.

Elements of Nearctic origin illustrate 2 patterns of mainland distribution: a) species distributed throughout the peninsula, including *Pyrgus albescens, Pieris protodice, Colias eurytheme, Strymon melinus, Celastrina Iadon, Apodemia mormo, Calephelis wrighti, Vanessa cardui,* and *Vanessa annabella,* comprising approximately 39% of the butterfly fauna; and b) species typically confined to the Californian province of the adjacent peninsula, represented on Cedros by disjuncts or isolated relict populations, including *Pieris beckerii, Anthocharis sara, Anthocharis cethura, Mitoura cedrosensis* new species, *Philotes sonorensis,* and *Euphilotes battoides.* All of these Californian elements reach their southernmost distributional limits on Cedros. Included in this group are the 2 endemic taxa. The Californian province elements account for approximately 26% of the species recorded from the island. Thus were it not for a broad zone of distributional overlap between the widespread Neotropical and widespread Nearctic species, the island's fauna would most likely reflect an even more depauperate conditon than is currently illustrated.

Approximately 50% of the species known from the adjacent mainland (species pool) occur on Isla de Cedros. This is consistent with the finding of Langston (1980) regarding the faunal composition of Santa Cruz Island which is located off the western coast of California. The two islands share 9 species of butterflies representing widespread Neotropical, widespread Nearctic, and Californian province elements. The species in common all exhibit a high degree of vagility.

Latitude seems to have little effect on the phenology of the Californian elements. Although Isla de Cedros is 500 km (310 mi) south of the California-Baja California border, species' flight periods closely resemble those of their southern California counterparts. Several of the univoltine species do, however, exhibit extended flight periods giving the appearance of more than a single brood, i.e., *Philotes sonorensis* and *Euphilotes battoides.* Langston (1975) has shown that species occurring near the Pacific coast (of California) often display this tendency, probably in response to mild winters, periods of inclement spring weather, and moderate summer temperatures, which in turn contribute to the staggered development of the various larval hostplants.

We examined 457 specimens representing 23 species. An additional 2 species, *Danaus plexippus* (L.) and a large dark papilionid, both reported as sight records by David Weissman, are mentioned here but are not included in the species accounts. All observations were made by the authors during 1981 and 1983.

Unless otherwise indicated, all specimens listed in the species accounts were collected by Faulkner and Brown, and are deposited in the San Diego Natural History Museum. Specimens collected by J. Garth are in the collection of the Allan Hancock Foundation at the University of Southern California, Los Angeles. Additional depositories are abbreviated as follows: CAS, California Academy of Sciences, San Francisco; and LACM, Los Angeles County Museum of Natural History.

Species Accounts

HESPERIIDAE

1. *Erynnis funeralis* (Scudder and Burgess).

First reported from Cedros by Rindge (1948), we collected *E. funeralis* on both the north and south ends of the island. It was encountered more often at mid-to-low elevations, frequently "patrolling" canyons. Several species of *Lotus* (Fabaceae) occur on the island, and one or more of these probably serve as larval hosts. *E. funeralis* occurs the entire length of the peninsula of Baja California, and there appear to be no phenotypic differences between mainland and insular populations.

MacNeill (1975) indicates that *funeralis* has considerable dispersal ability and has been shown to be a pioneer species in several insular situations.

Specimens examined: Punta Norte, 30 March 1983 (2 males), 1 April 1983 (2 males); vicinity El Pueblo, 4 April 1983 (1 female).

2. *Pyrgus albescens* Plötz

MacNeill (1975) states that *P. albescens* and *P. communis* (Grote) are ecologically isolated as well as (genitalicly) distinct. On this basis, they appear to represent separate species and were treated as such by Miller and Brown (1981). That treatment is followed here.

P. albescens is a widespread inhabitant of the hot, arid lowlands of the southwestern United States and adjacent Mexico. It was one of the more common butterflies encountered on Cedros in both spring and summer of 1983. It was particularly abundant in disturbed areas in the vicinity of El Pueblo, especially in association with the weedy, introduced *Malva parviflora* L. (Malvaceae). Several specimens were also collected on the south slope of Cerro de Cedros, near the summit, in association with *Sphaeralcea fulva* Greene (Malvaceae). No phenotypic differences are apparent between peninsular and insular populations.

Specimens examined: El Pueblo, 29 March 1983 (1 male), 4 April 1983

(10 males), 13 July 1983 (2 males); Punta Norte, 31 March 1983 (1 female), 1 April 1983 (1 male, 1 female), 3 July 1983 (2 males); vicinity Cerro de Cedros, 3 April 1983 (4 males, 1 female), 1 July 1983 (2 males); Gran Cañon, 2 July 1983 (1 male).

PIERIDAE

3. *Pontia protodice* Boisduval and LeConte

As *P. protodice* occurs commonly throughout much of the United States and northern Mexico, and in a variety of habitats, it was not surprising to find this species on Isla de Cedros. Specimens were collected on both the north and south ends of the island. Some of the possible cruciferous hosts available include *Descurainia, Sisymbrium,* and *Thelypodium.* Although seasonally polyphenic, *P. protodice* is quite homogeneous in phenotype throughout its range (no subspecies), including Isla de Cedros.

Specimens examined: vicinity Punta Norte, 28 February 1941 (1 male), *leg*: J. Garth, 30 March 1983 (1 male), 1 April 1983 (1 male); vicinity El Pueblo, 3 April 1983 (1 female), 4 April 1983 (3 males).

4. *Pontia beckerii* Edwards

A common pierid of the western United States, *P. beckerii,* generally inhabits hot, shrubby, semi-arid habitats (Howe, 1975). Only in southern California and northwestern Baja California does it occur on or near the coast. The population on Cedros represents a slight southern disjunct from northern Baja California. The larval host, *Isomeris arborea* Nutt. (Capparidaceae), occurs commonly on the eastern side of the island (Hale, 1941); a single larva was collected on *I. arborea* in a disturbed area near El Pueblo. Specimens of *P. beckerii* from Cedros are indistinguishable from those of southern California.

Specimens examined: El Pueblo, 29 March 1983 (2 males), 3 April 1983 (1 male, 1 female), 4 April 1983 (1 female); Punta Norte, 1 April 1983 (1 female); vicinity Cerro de Cedros, 1 July 1983 (2 males).

5. *Anthocharis sara* Lucas

Widespread through the western United States, and extending south into northern Baja California, *A. sara* reaches its southernmost distribution on Isla de Cedros. Capture records from February through April may indicate two broods, as is the case in coastal southern California.

Although some insular populations from California are subspecifically distinct (Emmel and Emmel, 1973), specimens from Cedros appear to represent nominate *A. sara.* However, in about 10% of the male specimens, the black scaling at the posterior end of the bar located near the apical end of the DFW cell, extends basally forming a slight hook (Fig. 5). Although these individuals have a distinct appearance, this character is not consistent within the population sampled.

Specimens examined: vicinity Punta Norte, 25 February 1932 (2

males, 1 female), 28 February 1941 (1 male, 1 female), all *leg*: J. Garth, 30 March 1983 (10 males, 1 female), 31 March 1983 (3 males, 2 females), 1 April 1983 (7 males, 1 female), 2 April 1983 (5 males, 1 female); vicinity El Pueblo, 3 April 1983 (1 male).

6. *Anthocharis cethura* (Felder and Felder)

Restricted to the extreme southwestern United States and adjacent northern Mexico, *A. cethura* reaches its southernmost limit on Isla de Cedros. Although first collected on Cedros by John Garth in 1932, its occurrence there was not noted until Rindge's (1948) publication. In the spring of 1983 *A. cethura* was collected on both the north and south ends of the island. Although it was uncommon, generally observed singly in canyons or on hilltops, previous collectors have found it to be much more abundant. The authors collected a single larva on *Sibara pectinata* (Greene) Greene (Brassicaceae) which is widely distributed on Cedros. Other potential larval hosts available include *Thelypodium lasiophyllum* (Hook. and Arn.) and *Descurainia pinnata* (Walt.) (both Brassicaceae). Specimens from Cedros are probably best referred to nominate *A. cethura.*

Specimens examined: vicinity Punta Norte, 25 February 1932 (1 male), 28 February 1941 (12 males, 3 females), all *leg*: J. Garth, 31 March 1983 (1 male), 1 April 1983 (1 male), 2 April 1983 (1 male); vicinity El Pueblo, 29 March 1983 (1 male), 3 April 1983 (2 males).

7. *Colias eurytheme* Boisduval

This widespread species was encountered only sparingly on Cedros. Specimens were observed in spring and summer of 1983. The only example collected, however, was a damaged adult retrieved from a spider's web. Several legumes on the island are available as potential larval hostplants.

Specimen examined: vicinity Punta Norte, 3 July 1983 (1 female).

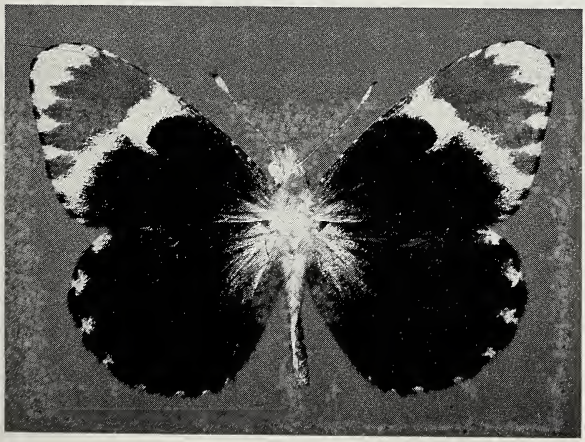


Fig. 5. *Anthocharis sara*, male, uppersurface, Isla de Cedros.

8. *Phoebis sennae marcellina* (Cramer)

Although probably not a breeding resident, *P. sennae* was commonly observed on both ends of the island in the summer of 1983. Captures were made in the late afternoon as the adults were settling on *Rhus*.

Larvae of *P. sennae* are known to feed on *Cassia* (Fabaceae), none of which are available on Cedros. A well-known disperser-migrator, *P. sennae* is frequently encountered far from its breeding areas, which appears to be the case on Isla de Cedros.

Specimens examined: vicinity Punta Norte, Cañon de la Mina, 3 July 1983 (2 males).

9. *Eurema nicippe* (Cramer)

E. nicippe is widespread throughout most of southern North America; it occurs the length of Baja California. As with the preceding species, *nicippe* does not appear to be a breeding resident on Cedros owing to the absence of *Cassia* as a larval host. It is possible that other legumes are utilized, but the flight-worn condition of specimens and their rapid unidirectional flight together seem to indicate that specimens taken on Cedros represent migrants from the adjacent mainland.

Specimens examined: vicinity Cerro de Cedros, 1 July 1983 (1 male); vicinity Punta Norte, Cañon de la Mina, 3 July 1983 (1 male).

LYCAENIDAE

10. *Mitoura cedrosensis* new species

Figures 6 and 7

Male: forewing length $\bar{x}$ = 11.4 mm (range 11.0-12.0 mm; n = 14). Frons and vertex fuscous; eyes mesially edged with white; antennae black, white annulate, the club black with a fulvous tip. **Upperside:** both wings fuscous to mahogany brown with marginal, apical, and basal darkening. A thin terminal white bar on hindwing between tornus and Cu_2. A short, thread-like tail at termination of Cu_2 of hindwing, black tipped with white. Only a small black tooth at Cu_1, also tipped with white. Forewing scent patch well developed although variable in color. **Underside:** forewing rich mahogany brown with a fine postmedian line composed of 5 white dashes. Faint traces of maroon purple over-scaling apically, and faint basal darkening. Hindwing with a diffuse inconsistent maroon postbasal band; occasionally bordered at outer margin by a thin white line from M_3 toward costal margin, absent to very faint in some specimens. Terminal area aqua gray with a variable row of poorly defined black dots. In Cu_1-Cu_2 a *Thecla* spot composed of 2 longitudinally arranged black dots divided by a poorly defined orange-brown lunule. Entire hindwing surface rather melanistic in appearance, with a faint iridescent luster.

Female: forewing length $\bar{x}$ = 11.4 mm (range 11.0-12.0 mm; n = 9). **Upperside:** as in male but without scent patch, and color more consistent rich reddish brown; darkening confined to marginal area. **Underside:** as in male with little or no consistent differences.

Fig. 6. *Mitoura cedrosensis*, female, uppersurface, Isla de Cedros.
Fig. 7. *Mitoura cedrosensis*, female, undersurface, Isla de Cedros.

Genitalia: Two specimens of each sex are illustrated in Figure 8. As noted by Brown (1983) for related species, variation, as exemplified between the two specimens of each sex examined, is substantial. Comparison with illustrations in Brown (1983) gives a brief account of the related southern California taxa. The only character which may be of diagnostic value is the dorso-ventral shape of the male saccus. The female genitalia and male valvae appear to be of less taxonomic value, although quantitative differences may be evident in larger samples which could be statistically validated. Although the saccus shape may be of diagnostic value in differentiating the *loki, thornei*, and *nelsoni* groups, this character does not lead to any conclusions regarding reproductive isolation (Shapiro, 1978).

Type material: All Isla de Cedros, Baja California Norte, Mexico; holotype, male, Punta Norte, 28°22′N, 115°12′W, 20-22 March 1981; allotype, Punta Norte, 28°22′N, 115°12′W, 20-22 March 1982. Thirteen male and 8 female paratypes as follows: Punta Norte, 20-22 March 1981 (6 males, 5 females), 1 April 1983 (2 males, 1 female), 31 March 1983 (3 males, 1 female), 30 March 1983 (1 male), 3 July 1983 (1 male); vicinity Cerro de Cedros, 1 July 1983 (1 female).

Disposition of types. Holotype and allotype are deposited in the SDNHM. Paratypes deposited in the following institutions: Los Angeles County Museum of Natural History, Los Angeles, California; California Academy of Sciences, San Francisco, California; and Universidad Biología de Mexico, Mexico City, Mexico.

Remarks. *Mitoura cedrosensis* is closely related to *M. loki* (Skinner). It represents an insular, southernmost outpost of the California juniper-feeding *Mitoura* complex and is endemic to Isla de Cedros. The nearest known population of *M. loki* occurs approximately 300 km to the north in the vicinity of Mike's Sky Ranch in the Sierra San Pedro Martir, Baja California Norte.

M. cedrosensis is easily distinguished from *M. loki* by its smaller size[1] and by the fuscous purplish brown of the ventral hindwing surface replacing the hindwing green overscaling of *loki*. When compared to the newly described *M. thornei* Brown (1983) from southern California, *M. cedrosensis* is smaller and the markings on the hindwing are slightly darker, more fuscous, and less well-defined. The thin, white border at the outer edge of the postbasal band present in both *thornei* and *loki* is reduced or absent in *cedrosensis*. There is some question regarding the specific status of *thornei* and *cedrosensis*, both of which might be considered as subspecies of *M. loki* by some authors (Shields, 1984). *M. cedrosensis* is not similar to the unusual *M. nelsoni* (Boisduval) known from Isla Guadalupe, Baja California Norte, Mexico (Powell, 1958; Brown, 1983). The presence of basal markings representing the inner

[1]Student's t-test comparing 2 sample means indicates statistically significant difference in forewing length between samples of *M. loki* and *M. cedrosensis* ($P < 0.001$).

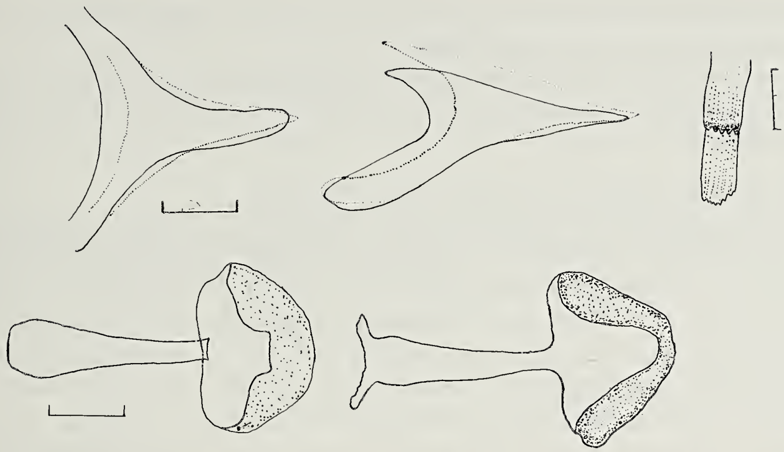


Fig. 8. Selected characters showing variation in male and female genitalia in *Mitoura cedrosensis*. **Upper Row, Left**: Dorsal view of saccus; **Right**: lateral view of valva. Saccus and valvae outlined by solid line in first specimen and dotted line in second. **Center Row**: Cornuti (both specimens identical). **Bottom Row**: Female, ductus bursa (sclerotized) and lamella antivaginalis.

margin of the postbasal band (hindwing underside) clearly separates *M. cedrosensis* from any *M. nelsoni* or *M. siva* (Edwards) populations.

Adults of *M. cedrosensis* were found in close association with California juniper (*Juniperus californica* Carr., Cupressaceae), which is undoubtedly the larval host (Brown and Faulkner, 1984). A captive female readily oviposited on the juniper, but the eggs were not viable.

California juniper, which generally exhibits a medium tall stature, grows almost prostrate in the canyons and slopes of the north end of the island. This aspect is so striking that the juniper was originally thought to be an endemic species closely related to *J. californica* (Gentry, 1950). Large stands of the juniper occur in scattered areas throughout much of the island, and it is suspected that the *Mitoura* has a distribution comparable to that of its larval host. Adults were collected in both the spring and summer probably representing 2 broods, consistent with other low elevation southern California *Mitoura* populations, i.e., *M. loki* and *M. thornei*.

11. *Strymon columella istapa* (Reakirt)

All specimens of *S. columella* taken on Cedros were collected on hilltops or prominent knolls in the area northwest of El Pueblo on the south end of the island. The larval hostplant in southern California, *Sida hederacea* (Dougl. ex Hook.) Torr. (Malvaceae), is not known from Cedros, but several other malvaceous plants are present. Although currently referred to *S. columella istapa*, specimens from Baja California and adjacent southern California are undoubtedly subspecifically

distinct from mainland *istapa* (Clench, *in litt.*). Insular and peninsular specimens are indistinguishable.

Specimens examined: vicinity El Pueblo, 29 March 1983 (1 male), 3 April 1983 (1 male); vicinity Cerro de Cedros, 1 July 1983 (5 males, 1 female).

12. *Strymon melinus pudica* (Hy. Edwards)

S. melinus is probably the most widespread Nearctic hairstreak. It occurs throughout much of the United States, extending into northern Mexico, and occupies a tremendous variety of habitats from mountains to deserts. *S. melinus* was first reported from Cedros by Rindge (1948), and it was encountered commonly in both spring and summer of 1983. This insect is a frequent hilltopper and was collected on both ends of the island. A number of potential larval hosts are available including *Malva, Phaseolus*, and *Eriogonum*. Larvae were abundant on the flower heads of the endemic *Eriogonum molle* Greene (Polygonaceae) in the summer of 1983. All Baja California material is best referred to subspecies *pudica*.

Specimens examined: vicinity Punta Norte, 28 February 1941 (1 male *leg*: J. Garth, 30 March 1983 (2 males, 1 female) 31 March 1983 (1 male), 1 April 1983 (3 males), 3 July 1983 (1 female), ex-larva, emerged 25 July 1983 (1 female), ex-larva, emerged 31 July 1983 (1 male); vicinity El Pueblo, 29 March 1983 (10 males), 3 April 1983 (2 males, 1 female), 4 April 1983 (2 males); vicinity Cerro de Cedros, 1 July 1983 (2 males, 6 females); Gran Cañon, 2 July 1983 (2 males); Punta Prieta, 5 July 1983 (2 males).

13. *Brephidium exilis* (Boisduval)

B. exilis occurs throughout Baja California, ranging from the coasts to the deserts and from Tijuana to La Paz. On Cedros it was most commonly encountered in heavily disturbed areas where weedy *Atriplex* and *Chenopodium* (Chenopodiaceae) formed dense clumps. Two such habitats include the vicinity of the fishing village at Punta Norte, and near El Pueblo at the south end of the island. Specimens from Cedros are indistinguishable from those collected elsewhere on the peninsula. *B. exilis* is also known from all the California Channel Islands (Miller, 1984).

Specimens examined: vicinity Punta Norte, 25 February 1932 (1 male), 28 February 1941 (1 female), both *leg*: J. Garth; Punta Norte 20-22 March 1981 (1 male, 1 female), 30 March 1983 (1 male, 1 female), 1 April 1983 (2 males, 1 female), 2 April 1983 (1 female); vicinity El Pueblo, 29 March (1 male, 1 female), 4 April 1983 (3 males), 13 July 1983 (1 female); Morro Redondo, 5 April 1983 (1 male); Cerro de Cedros, 1 July 1983 (1 male); Gran Cañon, 2 July 1983 (2 males, 1 female).

14. *Leptotes marina* (Reakirt)

L. marina was first reported from Cedros by Rindge (1948). Although not collected by us in the spring, *L. marina* was quite common in the

summer of 1983. This species occurs on both the north and south ends of the island, particularly in the lowlands and in disturbed areas. *L. marina* ranges the length of Baja California, extending north into California; it has also been collected on Santa Catalina, Santa Cruz, and Anacapa Islands (Emmel and Emmel, 1973; Langston, 1980; Miller, 1984).

Specimens examined: vicinity Punta Norte, 25 February 1932 (1 male), *leg*: J. Garth, 3 July 1983 (2 males, 1 female); vicinity Cerro de Cedros, 1 July 1983 (2 males, 1 female).

15. *Hemiargus ceraunus gyas* (Edwards)

Although quite rare and localized in the spring, *H. ceraunus* was abundant and widespread in the summer of 1983. This species was collected almost everywhere on the island, although most commonly at low elevations.

H. ceraunus gyas is distributed the length of Baja California and in a variety of habitats. It is multiple brooded and several genera of Fabaceae, including *Astragalus*, which is available on Cedros, are utilized as larval hosts.

Specimens examined: vicinity Punta Norte, 25 February 1932 (1 female), *leg*: J. Garth, 3 July 1983 (5 males, 1 female); Punta Morro Redondo, 5 April 1983 (5 females); vicinity Cerro de Cedros, 1 July 1983 (16 males, 6 females); Gran Cañon, 2 July 1983 (2 males, 1 female); Punta Prieta, 5 July 1983 (6 males); El Pueblo, 13 July 1983 (1 male).

16. *Philotes sonorensis* (Felder and Felder)

Restricted to California and adjacent Baja California, *P. sonorensis* reaches its southernmost limit on Isla de Cedros, slightly disjunct from the nearest peninsular population. First collected on Cedros by J. Garth in 1941, *P. sonorensis* was quite common in the canyons of the north end of the island in the spring of 1983. Typically one of the earliest spring fliers in coastal areas peaking in February and March, our captures in late March and April seem unusually late; the July record is extraordinary. Several species of *Dudleya* (Crassulaceae) are available as larval hosts; a single larva was observed feeding on *Dudleya pachyphytum* (Moran and Benedict, 1981).

Specimens examined: vicinity Punta Norte, 28 February 1941 (1 male), *leg*: J. Garth, 20-22 March 1981 (3 males, 1 female), 30 March 1983 (4 males), 31 March 1983 (7 males), 1 April 1983 (8 males), 3 July 1983 (1 female).

17. *Euphilotes battoides garthi* Mattoni

Rindge (1948) first reported *E. battoides* from Cedros; he also recognized that this insular population was phenotypically distinct. Shields (1975) later referred to two males from Cedros as conforming to his description of *E. battoides allyni*. Mattoni (1988) recently described the Cedros population as *garthi*, and examined its relationships within the *bernardino* cluster of subspecies.

E. battoides garthi is endemic to Isla de Cedros and probably occurs throughout the island wherever *Eriogonum fasciculatum* (Benth.) (Polygonaceae) is found. We encountered it most frequently in the canyons and washes of the north end of the island in spring 1983. *E. battoides garthi* represents the southernmost subspecies of the *E. battoides* complex. The nearest *battoides* population occurs about 130 km northeast in the northern central desert region of the peninsula (Brown and Faulkner, 1984).

Specimens examined: canyons west of Punta Norte, 30 March 1983 (2 males), 1 April 1983 (5 males, 4 females), 2 April 1983 (1 male), 1 July 1983 (1 male, 1 female), 3 July 1983 (2 females); Cedros Island, no further locality data, 15 March 1939 (3 males), no *leg* data, LACM, 18 March 1939 (1 female), no *lge* data, CAS.

18. *Celastrina ladon echo* (Edwards)

C. ladon echo, the westernmost subspecies of the widespread Nearctic *ladon* complex, has an extensive range from British Columbia to Baja California (Langston, 1975). It is also known from several islands off the western coast of California (Emmel and Emmel, 1973; Langston, 1979; Miller, 1984). The population on Cedros represents an isolated and disjunct outpost. The echo blue was the most common lycaenid encountered on Cedros; in the spring of 1983 it was particularly abundant in the canyons and washes of the north end of the island; and in July 1983, it was most common in the vicinity of Cerro de Cedros. The abundance of freshly emerged adults in both spring and summer indicates that the species is at least double brooded on Cedros. Larval hostplants encompass several families and many genera including *Rhus* and *Lotus*, both available on Cedros.

Specimens examined: vicinity Punta Norte, 25 February 1932 (2 males, 2 females), 28 February 1941 (21 males, 3 females), *leg*: J. Garth, 20-22 March 1981 (1 female), 30 March 1983 (6 males, 2 females), 31 March 1983 (6 males, 1 female), 1 April 1983 (2 males, 2 females), 2 April 1983 (4 males), 3 July 1983 (2 males, 2 females); vicinity Cerro de Cedros, 1 July 1983 (3 males); Gran Cañon, 2 July 1983 (1 male, 2 females).

RIODINIDAE

19. *Apodemia mormo virgulti* Behr

Figures 9 and 10

A dark segregate of *Apodemia mormo virgulti* with greatly reduced hindwing orange occurs in central and north central Baja California. Opler and Powell (1961) have indicated that these dark populations may warrant subspecific recognition. Specimens from Cedros are consistent in maculation and color, and represent the extreme in this phenotype.

Fig. 9. *Apodemia mormo virgulti*, female, uppersurface, Isla de Cedros.
Fig. 10. *Apodemia mormo virgulti*, female, undersurface, Isla de Cedros.

Apodemia mormo occurs in the canyons and washes of the north end of the island, generally associated with *Eriogonum fasciculatum* (Benth.) (Polygonaceae). It is known from the south end but is much less common there. The presence of *A. mormo* adults from March through July appears to illustrate the extended flight periods of coastal species previously suggested by Langston (1975). Although *A. mormo* extends all the way to the cape region of the peninsula, in the form of *Apodemia mormo maxima* (Weeks), Isla de Cedros is near the southernmost distribution of the *virgulti*-like phenotype.

Specimens examined: Punta Norte, 20-22 March 1981 (15 males, 5 females), 30 March 1983 (2 males), 31 March 1983 (2 females), 1 April 1983 (1 male, 1 female), 2 April 1983 (1 female), 3 July 1983 (1 male, 3 females); vicinity Cerro de Cedros, 1 July 1983 (1 male, 1 female).

20. *Calephelis wrighti* Holland

C. wrighti occurs throughout Baja California. First collected on Cedros by Hanna and Slevin in 1922, *C. wrighti* was one of the more common butterflies that we encountered in 1983. It was collected on both the north and south ends of the island, commonly in association with *Bebbia juncea* (Benth.) Green (Asteraceae), the larval host.

Considerable confusion exists in older literature between *C. wrighti* and *C. nemesis* (Edwards). Rindge's (1948) records of *Calephelis nemesis australis* (Edwards) from Cedros are almost certainly misdetermined specimens of *C. wrighti*.

Specimens examined: Cedros Island, 22 July 1922 (1 male, 1 female), *le*: Hanna and Slevin, CAS; El Pueblo, 29 March 1983 (1 male, 1 female), El Pueblo, 3 April 1983 (2 males, 1 female), 4 April 1983 (3 males, 4 females); Punta Norte, 30 March 1983 (2 males), 31 March 1983 (2 females), 2 April 1983 (1 male); Gran Cañon, 2 July 1983 (2 males); Punta Prieta, 5 July 1983 (1 male, 1 female).

NYMPHALIDAE

21. *Vanessa cardui* (Linneus)

In the spring of 1983 *V. cardui* was abundant throughout southern California and northern Baja California, exhibiting one of its periodic unidirectional migrations. The butterfly was extremely common on Cedros, with both flight-worn and freshly emerged adults evident. Larvae were plentiful on both the weedy *Malva parviflora* L. (Malvaceaae) and *Lupinus sparsiflorus* Benth. (Fabaceae). In years of exceptional abundance such as 1983, an extremely wide variety of larval hostplants are exploited by *V. cardui* (Emmel and Emmel, 1973).

First reported from Cedros by Rindge (1948), *V. cardui* is commonly encountered throughout the peninsula of Baja California.

Specimens examined: vicinity Punta Norte, 28 February 1941 (4 males, 2 females), *leg*: J. Garth; El Pueblo, 29 March 1983 (1 male, 2 females), 4 April 1983 (1 male), ex-larvae, ex-*Lupinus*, (4 females) emerged as follows: 20 April 1983, 19 April 1983, 18 April 1983, and 16 April 1983; Punta Norte, 30 March 1983 (4 males, 6 females), 31 March 1983 (1 male, 1 female), 1 April (1 female), 2 April 1983 (1 male, 1 female); vicinity Cerro de Cedros, 3 April 1983 (1 female).

22. *Vanessa annabella* (Field)

Another of the widespread vanessas, *annabella*, was encountered in large numbers on Cedros in the spring of 1983. It was particularly common at low elevations and in disturbed areas. *V. annabella* occurs the length of the peninsula of Baja California; insular and peninsular specimens are indistinguishable. *Vanessa virginiensis* (Drury), a notorious pioneer species present in many insular situations, was absent from Cedros; its hostplant, *Gnaphalium*, is known from the island.

Specimens examined: Punta Norte, 30 March 1983 (1 female), 31 March 1983 (1 male, 1 female), 1 April 1983 (1 female), 2 April 1983 (2 females); El Pueblo, 29 March 1983 (2 males, 2 females), 4 April 1983 (2 males, 1 female); vicinity Cerro de Cedros, 1 July 1983 (1 male).

DANAIDAE

23. *Danaus gilippus strigosus* (Bates)

A common inhabitant of the desert regions of southern California and Arizona, the striated queen occurs the length of the peninsula of Baja California, and in a variety of habitats. Although rather uncommon in the spring, with 1 or 2 individuals observed each day, *D. gilippus* was quite common in the summer of 1983 on both ends of the island. This species was reported from Cedros by Rindge (1948); his record is from the fall when the butterfly is probably more common. The only potential larval host available on Cedros is *Asclepias subulata* Decne. (Asclepiadaceae). Specimens of *D. gilippus* collected on the island may represent breeding residents as well as strays from the mainland.

Specimens examined: Punta Norte, 1 April 1983 (2 males) vicinity El Pueblo, 4 April 1983 (1 male); vicinity Cerro de Cedros, 1 July 1983 (1 female).

Discussion and Summary

Isla de Cedros supports an exceedingly depauperate butterfly fauna, primarily as a consequence of a limited mainland species pool. The Viscaino-Magdalena region of the peninsula directly adjacent to Cedros, lies near the southern end of the Californian Province influence, and considerably beyond the northern extremity of the Cape Province influence.

The biotic diversity of the Californian Province attenuates north of Isla de Cedros, with strays rarely occurring as far south as 28°N. Seasonal meteorological patterns do not favor immigration from this direction. Californian elements present on Cedros presumably represent relict populations separated from their contiguously distributed mainland populations since the Pleistocene.

Most of the Neotropical species inhabiting the Cape Region scarcely extend northward into the Viscaino Desert. Even such well known dispersers as *Phoebis agarithe* and *Ascia monuste* are yet to be recorded from Cedros. Apparently the combination of the Viscaino Desert and the Pacific Ocean together present an almost impenetrable barrier to Cape Province species' immigration to the island. The lack of suitable larval hostplants would also act to preclude these species from establishing in the event they were to be introduced to the island. Elements of Neotropical affinity present on Cedros represent widespread species occurring from Central America northward to at least southern California.

A speculative explanation for the conspicuous absence of butterflies common to the Californian province, such as *Icaricia acmon, Everes amyntula, Callophrys dumetorum*, and representatives of the genus *Satyrium*, can be extracted from the equilibrium theory of island biogeography. Since most of the above species occur sympatrically in cismontane Baja California with many of the island's resident species, it is possible that several of these missing butterflies were formerly resident on the island. Their absence may be partially explained by the reduction in floral and faunal diversity of the island which occurred as a result of its over-saturated biota following its separation from the Baja California peninsula. Many of the expected but absent species may have gone extinct on Cedros, and because prevailing conditions did not favour southward dispersal, were never reintroduced.

According to Pielou (1979), a low species diversity exists on islands not only as a function of land area and distance from the mainland, but also with aspects of community complexity acting to maintain this status. The fragmentary or patchy occurrence of suitable larval host-

plants makes it difficult for immigrant species of moderate host specificity to become established. The effects of patchy habitats in insular situations are discussed by Powell (1981) regarding the introduction of insect species onto Santa Cruz Island, California.

It should also be noted that man's presence on and his introduction of herbivores to Isla de Cedros has had little impact on the island's native flora and fauna. Man's activities have been restricted to the southeastern end of the island and in a lesser degree to the areas in and around the fishing village and abandoned copper mine on the northeast end. There is no current effort at agriculture, and its inherent ecological impact, owing to the poor soil conditions and undependable rainfall. There is barely enough groundwater from springs to provide for the growing needs of the village population, with none available for irrigation. Feral grazing animals, especially goats and pigs, are restricted to the southeast end of the island and have overall resulted in only minor impact on the island's native vegetation. This point is in sharp contrast to the effect that uncontrolled feral animals, mainly goats, have had on the flora of other Coastal Pacific islands, such as Santa Catalina Island (Coblentz, 1980) and San Clemente Island (Faulkner, personal observation) in California, and Isla Guadalupe (Moran and Lindsey, 1950) in Baja California, Mexico.

Acknowledgements. We thank John Garth of the Allan Hancock Foundation for sharing collecting notes and specimens he compiled during numerous visits to Isla de Cedros. We are also indebted to David Weissman for including us in a July 1983 collecting expedition to the island as well as the crew of the sloop Diamaresa, supplied by the Island Packers Company, Ventura, California, for providing transportation, meals, and lodging during the 2-week trip. Dr. Jerry A. Powell and Scott E. Miller both contributed significant editorial suggestions. Shirley Latislaw provided the map of Isla de Cedros and Rudolf H. T. Mattoni provided the genitalic drawings and discussions.

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Addenda. *Colias cesonia* Stoll has been documented recently from Isla de Cedros, bringing the species total to 24. The single record probably represents a stray from the peninsula rather than an indigenous population.

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Opinion.

Parallelism and Phylogenetic Trees

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Nearly all of Brock's (1988) statements in his criticism of my (Scott 1986) phylogeny of the advanced Ditrysia and Macrolepidoptera merely (but correctly) demonstrate that many character states of one Ditrysia group also independently occur in one or more other Ditrysia groups. But every worker on Ditrysia knows this; I knew of most of these independent occurrences when I wrote Scott (1986). Merely because there is a parallelism of a trait in several taxa does not invalidate the use of the trait as a shared derived trait for either taxon; if parallelism is real, the structure must by definition be a shared derived trait in each group in which it occurs. And most of the parallelisms that Brock cites involve primitive Ditrysia (Tineoid superfamilies or Cossoidea-Castnioidea-Zygaenoidea); one of the major points of Scott (1986) is that the phenetic distance between these lower Ditrysia and the Macrolepidoptera is so great that direct phylogenetic links between them are inconceivable. Brock fails to acknowledge the vast morphological gap (demonstrated by Scott 1986) between macrolepidoptera and lower Ditrysians such as Cossoidea-Castnioidea-Zygaenoidea and the Tineoid superfamilies; just counting the number of morphological differences between these groups and the Macrolepidoptera families clearly shows that they are not direct ancestors of any Macrolepidoptera, so parallelisms involving them are not directly relevant to Macrolepidoptera. Brock uses independent occurrence of many traits as justification for not proposing any phylogenetic scheme at all (his 1971 tree-like drawing resembling a phylogenetic tree was not derived from any list of characters using repeatable methods). But the fact of evolution means that the ancestor of every Ditrysia group had certain character states when it branched away from the remaining Ditrysia; therefore it is our job to deduce those character states were. Avoiding making a tree merely because of the complication of parallelism in some traits is not progress; progress is constructing trees and selecting the most likely tree, and listing the exact character changes involved so that other workers can verify or change the tree; progress is studying the characters in detail and the distribution of characters within taxa and reassigning those taxa that were misplaced (some reassignments may eliminate false parallelisms).

Brock's criticism (1988) also contains some misstatements of fact: Scott (1986) did not claim that secondary setae are absent in Noctuoidea; Scott wrote (p. 35) that "Noctuoidea . . . generally lack secondary setae" and his Table 1 shows that they are sometimes present. The Pyraloidea-Macrolepidoptera ancestor pupa was obtect in the sense

that only abdomen segments 5–6 moved. Sphingidae pupae occur in an earthen cell, but do any have true dense-silk cocoons? Hessel's (1969) figures clearly show that only Papilionoidea-Hesperioidea and some Cossidae have an aortic enlargement ("chamber"); the aorta is not enlarged much in other groups. The anapleural cleft IS a sulcus in Hesperiidae (fused, no longer a cleft). Abdominal segment 2 sternal apodemes are especially small in Rhopalocera. Maxillary palpi are 2-segmented in *Baronia* (Papilionidae) as well, but still they are very small in all Macrolepidoptera. Mandible remnants are not protuberant in Rhopalocera; in this group the name mandible remnant (and the erroneous name pilifer) does not represent an actual functional structure as it does in Cossoidea where the mandible remnants are definite bumps. Thus the name mandible remnant in Rhopalocera is not useful for morphological comparison, but is useful only for the convenience of Lepidopterist's descriptions; stating that mandible remnants are larger in Rhopalocera is misleading because the correct functional statement is that the sulci surrounding the absent "mandible remnant" are farther from each other. Lepidopterists' common practice of naming an ordinary expanse of exoskeleton as though it is some real functioning structure is frequently misleading; the truth is often that the area is just another undistinguished portion of body wall, and the functional structures that changed in the ancestor of the taxon are actually the sulci (which strengthen the cuticle during locomotion) or membranes (which allow movement of legs wings neck etc.)

Independently-possessed character states make the search for the true Ditrysia tree difficult, but do not justify the abandonment of the effort. Brock's comments do not mean that Scott's (1986) phylogenetic tree is wrong and should be changed. Brock should apply his expertise, and give us his phylogenetic tree, complete with character changes clearly placed on the branches of the tree (not some pseudo-phylogenetic gradistic tree conjured up with unknown methods, divorced from real data). And because parallelisms are common, perhaps a numerical taxonomy phenetic classification of the Ditrysia would be useful, merely to convince Lepidopterists that some superfamilies cannot be direct ancestors of some other superfamilies. I agree with Brock that too many Lepidoptera taxonomists refuse to apply their knowledge to study of phylogeny; these Lepidoptera taxonomists only seem to care about species/genera-level taxonomy, and once in a while they stray a bit by proposing a new obscure family; they "worship the god of genitalia" as they prepare drawings of the male and female genitalia that distinguish their species.

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Notes

A Significant New Hostplant record for *Pieris virginiensis* (Pieridae)

Since Klot's (1935, J. New York Entomol. Soc. 53:139-142) original description of the larva of *Pieris virginiensis*, this butterfly has been presumed to be monophagous, feeding exclusively on *Dentaria*. More recently, Shapiro (1971, Entomol. News 82:13-15) noted that the biology of this butterfly seemed completely tied to the phenology of its ephemeral hostplant. He found that in the laboratory, *P. virginiensis* females will oviposit on, and larvae will develop on several species of mustards. But that under natural conditions, *Dentaria* is the only host, probably because it is the only mustard which is usually present in this butterfly's habitat.

Chew (1980, Oecologia 46: 347-353) reiterated this position noting that populations with which she was familiar had only two species of mustards to choose between, *D. diphylla* Michx. and *D. laciniata* Muhl.. Likewise, the population studied in depth by Cappuccino and Kareiva (1985, Ecology 66:152-161) could choose between only these two hostplants. These authors quantitatively assessed and reaffirmed the close relationship between *P. virginiensis's* biology and the phenology of *Dentaria*.

In central Ohio, *P. virginiensis* occurs in isolated populations inhabiting wooded creek bottoms, usually with shale banks. In Morrow County, Ohio, we observed females ovipositing at a site where *Dentaria* is abundant in a creek bottom, but another mustard, *Arabis laevigata* (Muhl.) Poir, occurs as widely scattered plants on surrounding shale banks. From a distance, we noted *P. virginiensis* females settling on the *Arabis*, but we were unable to observe actual oviposition. However, upon examination, we found that these plants held several *Pieris* ova, presumably deposited by one or more of the females we observed. Later, by searching *Dentaria* we located two additional ova. Since all of these ova could have been deposited by *P. rapae*, which is also common in this area, we reared them on their original oviposition substrates. From these rearings we obtained two *P. virginiensis* pupae reared on *Dentaria* and one reared on *Arabis*.

These observations confirm the suggestion by Shapiro and Chew that *P. virginiensis* is usually monophagous not because female oviposit only on *Dentaria*, but because *Dentaria* is usually the only mustard available in their restricted habitat for them to oviposit on. Our preliminary observations indicate that *Arabis* may be more attractive to ovipositing females than *Dentaria*. Several *Arabis* plants located by us had several ova attached (one plant had six) while many *Dentaria* plants had to be searched to locate our two ova. However, *Arabis* is rare relative to *Dentaria* at this site, and we assume that *Dentaria* is the primary ovipositional substrate.

Arabis may be more attractive to ovipositing females, and because it is not as ephemeral as *Dentaria* it might allow more time for completion of larval development. However, its rarity in this habitat, and sometimes high egg load (indicating possible defoliation with no nearby mustards on which the larvae could relocate) limit the possibility that *P. virginiensis* could adopt a biological strategy that would allow it to become less dependent on *Dentaria*.

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Description of the Hitherto Unknown Female of *Acerbas suttoni* Russell (Hesperiidae)

The hitherto unknown female of *Acerbas suttoni* Russell is described as follows. The conspecificity of *A. latefascia* and *A. suttoni* are discussed below.
Acerbas suttoni Russell, 1984, Ent. Ber., 44:154-156; Figs 4a, b, 5, 6.
Female (Fig. 1): Forewing 20 mm. Head, palpi, ventral thorax, costa of legs, bases of forewing and ventral hindwing with green reflection. Antenna black, long, 3/5 length of costa. Abdomen dark brown; segments with faint white hairs on posterior margin. Dorsal forewing: dark brown, detached hyaline spots in spaces 2 and 3, small upper cell spot, no apical and lower cell spots. Dorsal hindwing: white median band from dorsum to vein 6, obscured in space 1b. Cilia brown, becoming paler toward tornus. Ventral forewing: similar to dorsal side, but dorsum paler. Ventral hindwing: blackish brown, median band conspicuous and sharply defined; break in space 1b; trace of band reach to costa.
Material examined: Lambarese, 100 km N. of Palopo, Sulawesi, Indonesia. 28. VI. 1966 (Bernice P. Bishop Museum, Honolulu).

Three species of *Acerbas* have been described from Sulawesi, of which only *A. azona* Hewitson, 1866 has been known for a long time. De Jong (1982, Ent. Ber., 42:88-90) described *A. latefascia* from one female specimen from N. E. Sulawesi. He suggested that *A. latefascia* could be considered a subspecies of *A. duris* Mabille, 1883, though he mentioned that the examination of the male would be necessary to establish the exact relationship of these two taxa. Two years later, Russell (1984, Ent. Ber., 44:154-156) described *A. suttoni* from one male from Central Sulawesi. He mentioned that A. *suttoni* was the nearest to A. *duris dorka* Evans, 1949 from Borneo in appearance. However, he did not suggest the relationship between *A. latefascia* and *A. suttoni.* I suggested (in litt.) the conspecificity of *A. latefascia* and *A. suttoni* to both of the authors before I found

Fig. 1 Female of *Acerbas suttoni*: dorsal and ventral view.

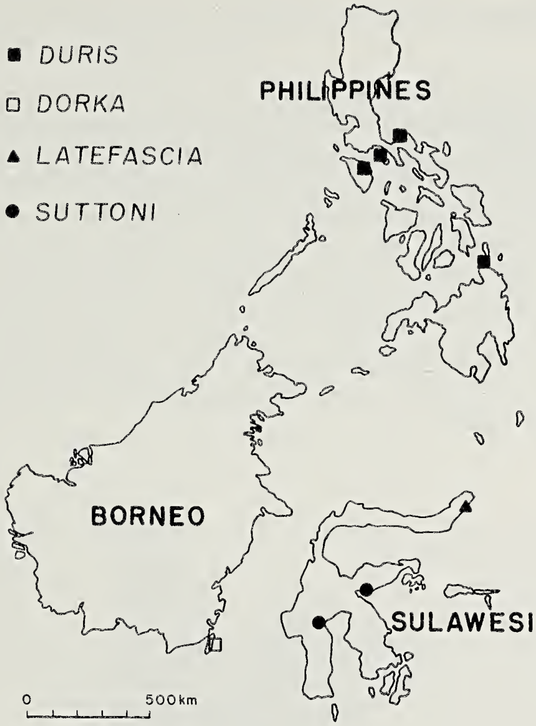

Fig. 2. Distribution map of *Acerbas duris* complex.

the female specimen described here in the Bishop Museum. De Jong (pers. comm.) suggested that further examination was necessary. Russell (pers. comm.) denied my suggestion because he felt that the two taxa were clearly differentiated and that only slight sexual dimorphism were known in this genus. After examining the male and the female of *A. suttoni* (I could not examine *A. latefascia* directly, but with a photograph), I retain my opinion that the two taxa could be the same species. The female markings do not differ markedly between *A. latefascia* and *A. suttoni*. The only significant difference is that the hindwing median band is clearer and wider in *A. latefascia* than in *A. suttoni*. This degree of difference, however, is not uncommon within intraspecific variation. Biogeographically, the two taxa are allopatric, and are, no doubt, congeneric with *A. duris* as both authors suggested (Fig. 2). I believe *A. latefascia* and *A. suttoni* should be treated as subspecies of a single species, but I withhold conclusive judgment. *A. suttoni* is now known from two males (the holotype and another in Tsukiyama collection in Japan) and the single female which are described here. *A. latefascia* is only known from single type female. Discovery of male *A. latefascia* is desirable to confirm my suggestion.

I thank H. Tsukiyama for permitting the examination of his collection, R. de Jong and A. Russell for useful comments. Special thanks to S. Miller for review of the manuscript and G. Uchida for photography.

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Homosexual Pseudocopulation in *Eucheira socialis (Pieridae)*.

Eucheira socialis Westwood is a bizarre endemic Mexican Pierid displaying a variety of degenerate morphological and behavioral traits associated with intense inbreeding and gregariousness (Shapiro et al., in preparation). Its mating behavior is extremely simplified; there is essentially no courtship; males approach and attempt to copulate with females, which either accept them or walk away rapidly. Both sexes mate multiply, and in some populations copulation may occur in the male-superior-dorsally position characteristic of Orthopterans and Coleopterans as well as most other non-Lepidopterous insects. Simultaneous multiple courtships of a single female are frequent, and at times males will attach to the side of the abdomen of an already-copulating female. Males have also been observed copulating with recently-dead females, and with each other.

Fig. 1. Living (right) and dead male *Eucheira socialis* in amplexus. The live male walked about vigorously dragging his dead partner.

The illustration (fig. 1) is of a homosexual pseudocopulation between two males from a single sibship originating in the state of Hidalgo, reared in the laboratory. The pair was first noticed at 1600 hrs, 2.VI.1987. At that time both males were alive. At 0900 the following day they were still in amplexus, but one was apparently dead. The photograph was taken at 1445, 3.VI; a few minutes later, under the influence of the strobe lights, the surviving male began to flap his wings violently and dislodged his burden. The dead male had been clasped tightly onto the living male to the left of the dorsal abdominal midline. There was no evidence of extrusion of any spermatophore material, and the survivor lived until 9.VI, the last three days in refrigeration.

Studies of *E. socialis* have been made possible by a grant from the UC MEXUS program.

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Effect of Refrigeration on Hatching of Eggs of the Tasar Silk Moth *Antheraea mylitta* Drury (Saturniidae)

Antheraea mylitta Drury is a semidomesticated Tasar Silk Moth with three generations a year: July-August, September-October and November-December. After the third broad, seed cocoons are preserved in commercial tasar insectaries until mid-June for egg production for first crop. During this period the pupae usually diapause from Winter (December-February) until the following summer (March-June). However, it has been recently observed that from May to mid-June emergence occurs which leads to the production of fertile eggs. Their resultant larvae cannot be reared due to lack of quality food plant leaves and excessive outdoor temperature (39±4°C). The situation requires means to preserve those unseasonal eggs until a favourable rearing time.

Considerable information is available on the effect of low temperature on mulberry (*Bombyx mori*) silkworm eggs (Yakoyama, 1962; Tanaka, 1964; Datta *et al*, 1972; Devaiah & Thontadarya, 1975; Govindan & Narayana Swamy, 1986; Narayana Swamy & Govindan, 1987; Tayade *et al* 1987) and eri (*Phibsamia ricini*) silkworm eggs (Govindan *et al*, 1980, Chowdhury, 1982; Vishwakarma, 1982-83), but no such literature is available on the Tasar silkworm eggs. Consequently an attempt was made to study the effect of refrigeration on hatchability of the eggs of Tasar Silk Moth *Antheraea mylitta* as follows.

29,000 freshly oviposited eggs were collected at random from healthy coupled female moths of the STV (Sukinda tri-voltine) race of *Antheraea mylitta* from Mayurbhanj district of Orissa, India on 22 May 1987. These were kept under room temperature (31 ± 2°C) as a common stock. Every day at 9 A.M., from the first to seventh day following oviposition, 4000 eggs were taken at random from the common stock and divided into four equal parts, each subjected to 24, 48, 72 or 96 hours of refrigeration (10 ± 1°C). Following treatment, the eggs were allowed to incubate at room temperature until hatching. The remaining 1000 eggs served as the control. The hatching percentage of the refrigerated eggs were noted and compared with the control. The experiment was repeated five times during the same period under the same conditions.

Results and summarized in Table 1. The control eggs kept at room temperature (31 ± 2°C) showed 82.44 percent hatch. The refrigeration of 0 day old eggs (fresh) for 24 and 48 hours indicated 82.34 and 82.28 percent hatch respectively, not significantly different from the controls. The same eggs when refrigerated for 72 & 96 hours showed reduction in hatching percentage. Cold treatment to 1 day old eggs for 24 hours also gave satisfactory hatching (82.32%), but in the other treatments, as 1 day old eggs refrigerated for 48, 72 and 96 hours and 2, 3, 4, 5, and 6 day old eggs refrigerated for 24, 48, 72 and 96 hours, there was reduced hatch.

The effect of refrigeration on *Antheraea mylitta* eggs of different ages indicated that the eggs beyond 1 day old were more susceptible to damage at lower temperatures. Vishwakarma (1982-83) observed that *Philosamia ricini* eggs beyond third to fifth day old were more susceptible to low temperature (7 ± 2°C). Datta *et al* (1972) found increasing percentage of mortality in *Bombyx mori* eggs under low temperature refrigeration (5 to 7°C). Govindan *et al* (1980) reported that refrigeration of *Samia cynthia ricini* Boisuduval eggs beyond 5 days old had adverse effect on hatching. Narayana Swamy and Govindan (1987)

Table 1. Mean Hatching percentage of *A. mylitta* eggs refrigerated for different time and at different ages.

Day after oviposition	Age of Eggs (Day)	HATCHING PERCENTAGE			
		24 hours refrigeration	48 hours refrigeration	72 hours refrigeration	48 hours refrigeration.
First	0 (Fresh eggs)	82.34	82.28	74.48	78.14
Second	1	82.32	42.62	24.54	26.86
Third	2	46.30	50.04	72.06	32.82
Fourth	3	72.26	62.74	63.26	46.10
Fifth	4	60.36	62.22	74.10	24.42
Sixth	5	76.38	74.54	56.26	62.38
Seventh	6	72.56	62.12	44.22	60.32

reported that the hatching percentage of *Bombyx mori* eggs of blue stage reduced with increase of refrigeration period from first day (83.70%) to the seventh day (21.60%).

In general, percentage of hatching of *Antheraea mylitta* eggs declined with increase of cold period with few exceptions (Table-1). A similiar trend was also observed by Datta *et al.* (1972) in *Bombyx mori* eggs. Tayade *et al* (1987) concluded that short refrigeration is better to minimise adverse effect on hatching percentage of *Bombyx mori* eggs. Narayana Swany and Govindan (1987) observed that the refrigeration of eggs of pure Mysore race of *Bombyx mori* at blue stage negatively affected yield. Govindan and Narayan Swamy (1986) reported that multivoltine silk worm eggs of *Bombyx mori* at eye spot stage can be refrigerated for one day without decreasing yield.

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A Melanic Aberration of *Philotes sonorensis* (Lycaenidae) from California

The Sonora Blue, *Philotes sonorensis* (Felder & Felder) with ts exquisite color pattern of iridescent light blue, black and white markings, and red spots, is one of California's most beautiful butterflies. Locally common in the nondesert portions of California, it is found in the mountains of Santa Barbara County,

Fig. 1. Aberrant *P. sonorensis*: left, dorsal; right, ventral

Fig. 2. Habitat of *P. sonorensis* in Mission Canyon. (see text to-spelling it is doubt)

flying in February-March of each year. The author has collected this Blue in Mission Canyon, in the Santa Ynez Mountains, and in Oso Canyon, in the San Rafael Mountains.

The Santa Ynez Mountains, predominantly chaparral-oak woodpland, form a 2,000 ft to 4,000 ft. wall behind the cities of Carpinteria, Santa Barbara, and Goleta Valley. Large colonies of *Philotes sonorensis* are to be found on its south slope. Mission Canyon is a large watershed below La Cumbre Peak where a number of small waterways converge to form Mission Creek, which runs down through the Santa Barbara Botanic Gardens, behind the Santa Barbara Museum of Natural History, through the city of Santa Barbara, and out to the Pacific Ocean. There is a bridge in upper Mission Canyon, which crosses the creek at the 1,400 ft. elevation, and above this bridge the foodplant, *Dudleya lanceolata* (Nutt.) Britt. & Rose. Crassulaceae is abundent on the rocky hillsides, and supports a large colony of this Blue. (Figure 2)

Here in Mission Canyon a male melantic aberration of *Philotes sonorensis*, was caught by Robert F. Denno, February 23, 1961. (Figure 1) This is a striking aberration, with the black spots on both the forewings and the hindwings smeared across the wings. Both wing surfaces are affected.

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A Replacement Name for *Lycaena editha nevadensis* Austin (Lycaenidae)

It has come to may attention that the name *Lycaena editha nevadensis* Austin (J. Res. Lepid. 23:83, 1984) is an invalid junior primary homonym of *Lycaena nevadensis* Oberthur (Etud. Ent. 20:pl. 4, fig. 54, 1986). To rectify this, I propose the following replacement name for *L. e. nevadensis*:

Lycaena editha obscuramaculata

The description, types and type locality remain as in Austin (1984, *op. cit.*: 83-88). The new name reflects the faintness of the maculation on the ventral hindwing, characteristic of the subspecies. At the time of the original description, specimens were known only from northern Elko and Humboldt counties, Nevada. Subsequently, I have examined material from southwestern Idaho (Canyon County, CM) and Ruby Valley, Elko County, Nevada (AMNH).

I thank C. A. Bridges for pointing out the homonymy to me and F. H. Rindge (American Museum of Natural History, AMNH) and J. E. Rawlins and C. W. Young (Carnegie Museum of Natural History, CM) for allowing me to examine specimens in their care.

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Sex Characters of the Pupae of the Banded Moth, *Cochylis hospes* Walsingham (Lepidoptera: Cochylidae)

The banded sunflower moth *Cochylis hospes* Walsingham, is a destructive pest of commercial sunflower seed (Charlet and Busacca 1986, Charlet L. D. and J. D. Busacca. 1986. Insecticidal Control of Banded Sunflower Moth, *Cochylis hospes* (Lepidoptera: Cochylidae), Larvae at Different Sunflower Growth Stages and Dates of Planting in North Dakota. J. Econ. Entomol. 79:648-650. Beregovoy, personal communication). Increased cultivation of the sunflower and economic loss due to banded sunflower moth damage has led to research into the biology and control of this species. A description of sex characters useful in sexing the pupae has not been published. Sexing the pupae is useful for behavioral or physiological research where adults must be kept separate. The genital primordia and the length or diameter of the antennae have been used to sex pupae of the sunflower moth *Homoeosoma electellum* Hulst (Rogers C. E. 1978. Sexing pupae and adults of the sunflower moth. S. W. Entomol. 3:305-307). These morphological characters were examined in the banded sunflower moth to determine their usefulness in sexing pupae.

Pupae were obtained from a laboratory culture of *C. hospes* established at the Metabolism and Radiation Research Laboratory, Fargo, North Dakota. A

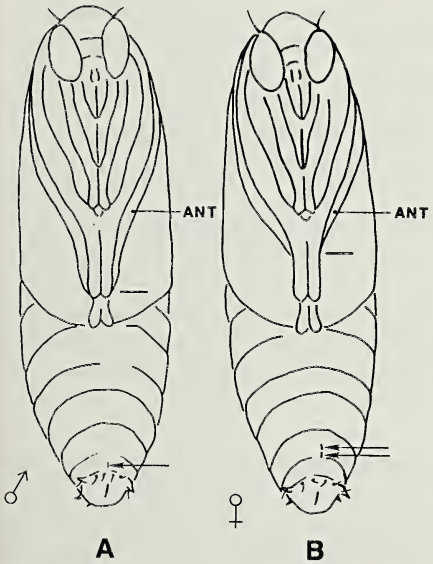

Fig. 1. Ventral view of *C. hospes* pupae showing sex characters Arrows show genital primorida. Solid lines indicate posterior limit of antennae. Ant = antenna

The genital primordia and length of the antennae are useful in sexing the pupae of *C. hospes*. The genital opening of the male pupae is a single opening on the 9th abdominal sternite (Fig. 1A). The genital opening of the female is on the 8th abdominal sternite. The female genital opening is longer than in the male and appears divided into two openings (Fig. 1B). The developing antennae extend to the margin separating the 2nd and 3rd abdominal sternites in females. In males, the antennae extend to the margin separating the 3rd and 4th abdominal segments (Fig. 1).

The genital primoridia are conclusive morphological features to identify the sex of *C. hospes* pupae. The lengths of the developing antennae are reliable sex characters, but experience is required to use this character. In the authors experience, these morphological features were 100% reliable.

dissecting microscope at 20X was used to examine 50 pupae. Conformation of sex in relation to morphology was determined by dissection of the pupa for testes and ovaries.

Reliable methods to sex *C. hospes* pupae should be useful in research on the behavior and biology of this important pest species.

Acknowledgements. The assistance of Kelly Jones and Sharon Grugel in rearing *C. hospes* in the laboratory is acknowledged.

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Laboratory Rearing of *Sandia xami xami* (Lycaenidae, Eumaeini).

The population dynamics of *Sandia xami* in a small volcanic area near Mexico City has been studied since 1984. The high numbers of eggs required to perform life-table experiments lead us to attemp the rearing of *S. xami* in laboratory conditions.

S. xami flies from central México to the southern part of Texas and Arizona (Scott, J.A. 1986. *The butterflies of North America*. Stanford University press. Stanford, California. 583 pp.). In the Valley of Mexico *S. xami* can be found all year with peaks of abundance in August-October, January-March and, perhaps, April and May (Soberón, J., C. Cordero, B. Benrey, P. Parlange, C. Garcia-Saez and G. Berges. 1988. *Ecol. Entom. 13(1)*: 71-76.). *S. xami* feeds on several Crassulaceae species (Ziegler, J.B. and T. Escalante. 1964. *Jour. Lep. Soc. 18*: 85-89) but in the ecological reserve on the National University of Mexico Campus at Mexico City, the main food plant is *Echeveria gibbiflora*. The larvae eats the leaves, flowers and stem of the plant. *S. xami* may be regarded as a leaf-miner on the exceptionally thick leaves of *Echeveria*. The life cycle was partially described by Ziegler and Escalante (*op. cit.*). The territorial behavior of *S. xami* has been described by Cordero (1986. Defensa territorial en la mariposa *Sandia xami*. B. Sc. Thesis. Fac. de Ciencias. UNAM. 75 pp.) and Cordero and Soberón (submitted) and their oviposition patterns by Soberón *et al* (*op. cit.*).

Early Stages

To obtain the eggs in the laboratory, a fertilized female is placed in a cage (fig. 1) built according to Munger, F. and T.T. Harris (1970. *Jour. Res. Lep. 8*: 169-176.). A 100 watts tungsten lamp is placed over the insectary a providing a 8:16 LD. One or two pots with *Echeveria* are placed inside the insectary. The females lay most eggs on the surface of the plant, although it is not uncommon to find eggs on the pot. A single female can produce up to 200 eggs in a three week period (fig. 2). Peak egg-laying takes place in the first week.

Every morning eggs are removed using a fine camel hair brush slightly dampened with tap water. The eggs are then placed in square (1.5 cm side) cuts of *Echeveria* leaves over a filter paper and inside plastic Petri dishes.

Larvae that have emerged from eggs are fed with squares of *Echeveria* which are replaced as required. The humidity inside the Petri dishes is kept high by a drop of water every three days. The Petri dishes are kept at room temperature. A single, medium-sized leaf (10 cm long) provides food for one larvae to mature.

Larvae are handled with fine camel hair brushes during the first two instars.

Later instars can be manipulated with coarse brushes or entomological forceps.

When larvae are ready to pupate, they stay still at the edge of the Petri dish and remain in this state for three to four days.

When adults are ready to emerge (16 to 20 days from beginning of pupation depending on temperature of the year, $\bar{x} = 16.9$ days, S.E. = 1.2), the pupae are placed in a closed plastic box with enough space for the spreading of the wings to take place.

Mortality is usually low at every instar, with the exception of the first. New larvae can be easily damaged by handling. A sumary of several laboratory life tables is presented in fig. 3.

The adults are maintained in the insectaries on a diet of 10% sucrose on water with a few drops of commercially available hydrolyzed vegetable proteins ("Jugo Maggi", trade mark, similar to soy sauce). Small cubes of plastic foam moisted with this solution are placed at the end of 10 cm wood sticks attached vertically to a base of clay. The adults must be placed by hand upon the foam cubes. This can be easily performed by gently persuading them to attach themselves to one finger and then placing the butterfly on the foam. At room temperature in Mexico City (around 20°C) adults can survive for as long as 40 days.

Mating

Inducing butterflies to copulate in laboratory conditions is seldom an easy task. Hand-pairing has been successful for large butterflies (Clarke, C.A. and P.M. Sheppard. 1956. *Jour. Lep. Soc. 10*: 47-53.), but the Lycaenids are more difficult to hand-pair because the genital armature is more deeply hidden than in other families (Clarke and Sheppard, *op. cit.*). We tried the hand-pairing methods, but none was successful. We have developed two techniques, described as follows.

1) We placed pairs of laboratory-raised butterflies in portable cages made of green net cloth and wire (fig. 4). These are then hung outside the laboratory, in direct sunlight. Matings occur within the hour. At first we used both wild-caught and laboratory specimens, but wild males always refused to mate. Seventeen attempts, during cloudless weather, using laboratory reared butterflies yielded 15 successful matings. The two failures were apparently due to female refusal because of unknown causes. This method works quite well, but it relies on availability of sunlight and, perhaps, on a good ventilation of the cages (R. Mattoni, personal communication).

2) It is also possible to obtain matings with males in the wild. Many territories are located in conspicuous places that are usually occupied by a male (Cordero, *op. cit.*; Cordero and Sberón, *op. cit.*). A laboratory female, one or two days old, is placed in a small card box with the lid attached to a string. The box is fixed to the end of a 1.5 m wood pole. The box is then placed as close as possible to the perching male and the lid opened by pulling the string. When the female emerges, a mating flight usually ensues, with a high probability of a successful pairing. In our area the vegetation includes *Buddleia* trees, which can be 4 or 5 meters tall. If the mating takes place on a tree, recapturing the couple may be impossible, but when the mating occurs in an accessible place, recapture after a period of 1 hour has always yielded a fertilized female. We have released 16 females and recovered 7 fertilized females.

Although this method requires the localization of an occupied territory and is less reliable than the first, it can be used to mantain heterozygocity.

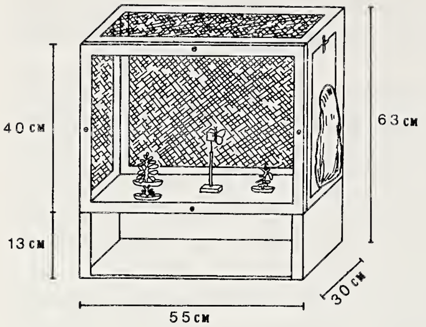

Fig. 1 Insectary for the maintenance and oviposition of adult *Sandia xami*, built according to Munger and Harris (1970).

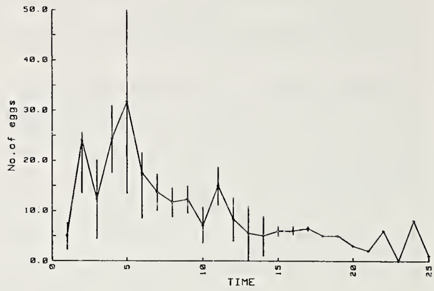

Fig. 2 Mean oviposition per day for female *Sandia xami*, in laboratory conditions with 8:16 LD light. The eggs were removed every morning. Mean ± standard error. N = 7.

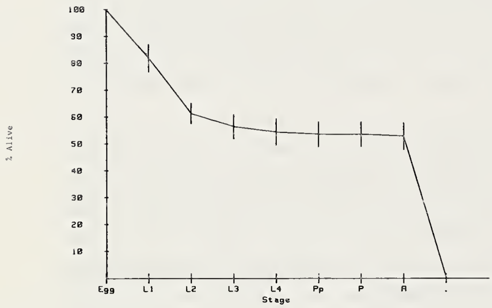

Fig. 3 Mean survivorship curve of seven laboratory life tables. Bars are standard errors. In parenthesis mean and standard error of duration of stage in days. Eggs (6.89 ± 0.07); L1 = first instar (5.36 ± 0.06); L2 = second instar (4.71 ± 0.07); L3 = third instar (5.40 ± 0.10); L4 = fourth instar (6.72 ± 0.13); Pp = prepupal larvae (3.70 ± 0.04); P = pupa (18.39 ± 0.25); A = adult (31.34 ± 1.18).

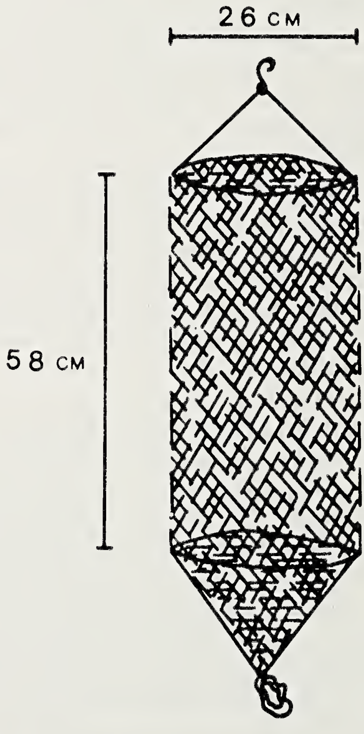

Fig. 4 Mating portable cage.

Acknowledgements. We are thankful to Dr. Jorge Llorente, of the Faculty of Sciences of the UNAM, and Dr. Kurt Johnson, of the American Museum of Natural History for their suggestion of the first method for inducing matings and Dr. Mattoni for his comments on this manuscript. Paulina Parlange, Betty Benrey, Gerardo Berges and Carlos Cordero were very helpful at different stages of this work.

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THE END OF NATURE: 1989. Bill McKibben. Random House, N.Y. 230 pp. $19.95

Armageddon 1: Nature O.

The End of Nature, a landmark book for this century on the philosophy of the relationship of man to the environment, was not written by a scientist, but by a reporter. To the academic clique this lack of credentials may be looked upon with suspicion, but the clarity of thinking, mastery of fact, cool objectivity and charm of writing are both very impressive and very moving.

I don't believe any of our members, who are almost universally in regular touch with nature, will fail to grasp or disagree with the central thesis of the book: nature has come to an end. Nature here is that idea describing the set of interactions among wild organisms that we think of as the planetary ecosystem. In the meantime we all go blithely consuming, travelling, and making investment decisions like life as we know it will all go on forever. In the meantime the almost certainly entrained global warming trend is signalling continuing disintegration of the environment with a foreseeable end to the lifestyles we have grown to accept. Deductions from the impact of human resource depletion is nothing new, of course, but what McKibben shows is that the wild nature in which we evolved is no more. We now live in a man-made world.

The destruction of nature is not only irreversible, but will in all likelihood be compounded by the "fixes" technology has and will generate. This pessimistic conclusion will probably not be accepted in the popular weltanschaung. The laws of nature, as thermodynamics and relativity, have not been repealed, many forests are still green, there are masses of moth species in some tropical places and there are a few aborigines around. But this is a managed home. My job with "restoration and management" of endangered species at the El Segundo sand dunes focuses on the absurdity. This tad of nature only now exists at our pleasure. The catena is gone.

You cannot fail to read this book. It is not strident or hysterical. There is no preaching or demands for change in life style. It is reflective, disturbing and very topical.

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PORTRAITS OF SOUTH AUSTRALIAN GEOMETRID MOTHS. McFarland, Noel. 1988. 400 pp. + inserts in pocket. Publ. by author, P. O. Box 1404, Sierra Vista, AZ 85636, USA. Price postpaid $80.00 USA, $85.00 outside USA. Softcover.

In the time of the closing of the american mind, along comes McFarland's Portraits as a refreshing throwback to a gentler kinder era. The price is a bit steep for a black and white, typewriter font softcover, but I recommend that you at least strongly urge your library to buy the work as a book you cannot live without. However, this should be done quickly, as I understand the limited 500 copies are selling well. Rationally, any success for so obscure a focus (geometrids of South Australia) is surprising, if not miraculous. The answer lies partly in the superb quality of the graphics. According to information the prints were processed with a 300 mesh screen. The results are the highest quality half tones around. The 10⅓ × 13¾ size delivers the figures as portrait scale, and there are about 1500 illustrations. The cover weight is no greater than this Journal, however, which makes the book awkward to handle, especially if one reads same in a lounge chair. The typewriter typeface of the text suggests a transitory presentation, but on refection may not be inappropriate for a work of this sort, which is more diary than scientific paper. That is its charm and value.

The natural history writing style is strictly descriptive, but is straightforward and clear. The exquisite detail and documentation provides minimal quantitative information, yet of its kind, every angle is covered. Further, the subject is pursued with a passion not only of the subject matter, but for the precision of the topic discussed. Casual asides provide an empathetic feel for working conditions: photographic equipment deluging Mrs. Henley's dining room table while chowing down on Andrew's fish and chips. The biology of the geometrids is completely covered for 72 species, each treated in its own "chapter" with morphology and behavior data of adult through egg, including parasites. Data on breeding technique are thorough to a fault, including considerations on failure. I would suggest no-one working with geometrids at any venue could do without this work.

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THE MOTHS AND BUTTERFLIES OF GREAT BRITAIN AND IRELAND. Volume 7, part 1, Hesperidae-Nymphalidae. The Butterflies. A. M. Emmet and J. Heath, eds. 1989. Harley Books, Colchester (England). 370 pp. 24 col. pl. £49.50.

This splendid book unquestionably is the new definitive text on british butterflies. The work is beautifully produced including painted color illustrations that are absolutely first class. The book may be regarded as an exemplar of its type. It is divided into three sections. The first is a chapter by A. M. Emmet on the early lepidopterists which gives the origin of the vernacular names of all species. Since the historical subject is regional, this part would

have limited interest to workers outside the U. K. It is noteworthy, however, that the common names of british butterflies have a long heritage and are remarkably stable, far more so than the scientific names (see below). The second, all too brief, chapter by M. G. Morris and J. A. Thomas is titled "Re-establishment of insect populations, with special reference to butterflies", but sets forth the topic of conservation as well. Because of the premier position of these authors in butterfly conservation, this chapter is must reading for all lepidopterists. The emphasis of these authors on the subject of re-introductions is fraught with opinion and tinged with some hostility, yet the points are righteous and very apt to the circumstances of diminishing biodiversity everywhere. The positions of Morris and Thomas are particularly close to me, for both trying to re-introducing butterfly species into a highly disturbed habitat and also attempting to restore a working ecosystem involving plants and other animals as well. Time and expense wasted in trivial arguments on myopic positions with bureaucrats brings their discussion home.

The major section of the book is descriptive. It assumes one is a knowledgeable student of the field. The systematic and distributional data are given in some detail including highlights of the life histories of all resident native species. The richest informational material lies in the distribution data, which is essentially presented in the form of 10 km sq UTM maps, with the time frame of occurrence categorized into pre-1940, etc. Maps for regular migrants present quantitative data. Every species ever recorded from Britain is cited, including some downright bizarre observations. Obvious escapes, as are apparently becoming more commonplace with the advent of butterfly houses, are omitted. The "natural" migrants are fascinating for information provided on potential vagility of different species. Historical evidence is summarized for species which were or could have been breeding residents in kinder and gentler times as *Aporia crataegi, Lycaena virgaureae* and *Cyaniris semiargus*. Thus the importance of these species beyond their curiosity status for collectors is validated. For future generations information on historic distributions of all organisms is extremely important, particular assuming a hopeful change in human behavior towards greater rationality in dealing with the conservation of nature.

In spite of all of its goodness, the book is not perfect. Perhaps its most damaging feature is the very spotty attribution of work cited, particularly in the sections dealing with biology. The bibliography is overall disappointing, based, no doubt, by the editors assuming the trail to more arcane works could be followed by the conscientious. The major attention to adult appearance substantially weakens the book, particularly as early stages are so well known for the british fauna. A key to mature larvae would have been simple and would not have materially added to length. Chaetotaxy maps of larvae with SEM micrographs are not unreasonable to expect from a work of this class given the resources and talent of its some 30 editors, associates, and authors.

In contrast to the stability of common names virtually since the time of Linneaus, the scientific name picture is disturbing. The use of *Eurodryas* is especially inappropriate, standing in sharp contrast to conservatism in the use of *Argynnis* and *Lycaena*. Although the nomenclature topic has been written into near banality, the strongest argument is for conservatism in a world where the primary objective of taxonomy is communication and stability and not the needs of specialists. A last criticism is the inaccessibility of informa-

tion. The recent guide by Thomas, *Butterflies of the British Isles*, employs a clever bar graph showing the phenology of life cycles. Thomas' presentation, combined with tables of foodplants, nectar sources, vagility, etc. in a few pages would impart information at a glance that otherwise requires lengthy rooting through the text. In spite of a few warts, lepidopterists everywhere can look forward to completion of the whole series as a landmark.

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PRIMITIVE GHOST MOTHS. 1989. E. S. Nielsen and N. Kristensen. Monographs on Australian Lepidoptera: Volume 1. 206 pp. + xii. CSIRO Publications. East Melbourne. $A60. Hardbound.

Here is a work of real systematic science in the event you are looking for a role model. Although *de facto* interest in Hepialids may not qualify them as a popular group, they are of great importance to understanding the phylogeny of Lepidoptera. This book only treats one genus, *Fraus* Walker, which includes only 25 species. Of these, 17 are newly described.

The general importance of the work, however, lies in the 116 pages of background material that prefaces the remainder of the book-the taxonomic revision proper. This background material includes a truly extraordinarily detailed morphology of all stages of the moths, but emphasizing the Adult. Included is a virtual atlas of both integument and internal anatomy illustrated by supurb SEM photographs. One cannot praise the quality of the illustrative material too highly, which appears in a total of 435 figures. A comprehensive biology review of 5 pages follows the 98 page morphology section, then 7 pages on diversity and distribution, and 4 on phylogeny. The latter includes a discussion on the overall classification of the Hepialidae and relationship of the family to other Lepidoptera. There is a cladogram of relationships, based on the thorough information presented herein.

The book is well produced and bound. It is obviously not a work for the general audience, but at least every institution involved with the systematics of Lepidoptera has the responsibility of acquiring this book. Every lepidopterist with concerns in morphology and/or primitive moths will find it invalueable. Note well the very reasonable price for a work of such high intellectual and physical standards.

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THE BUTTERFLIES OF HISPANIOLA, 1989, A. Schwartz, University of Florida Press, Gainesville, pp. 580.

Butterfly books that are based on an author's firsthand field experience occupy a special place on the bookshelf. Through this type of book one may

gain insight into how the butterflies of some exotic land look and act, and what they do for a living. In a summary of over ten years worth of field trips and museum work by himself and a score of field assistants, Albert Schwartz provides us with a new, hardcover book — *The Butterflies of Hispaniola.*

For the hard bitten types who buy butterfly literature this book may prove useful. Between the covers of *The Butterflies of Hispaniola* lie numerous flower visitation records, and a wealth of no nonsense locality, temperature and seasonality data on 196 species of butterflies. A colleague with experience assures me that to find a species of Hispaniolan butterfly, just use Schwartz's data — if the habitat hasn't been destroyed, the butterfly will be there. The taxonomy used in the book is a composite of the families employed by Riley (1975) and the generic names of Miller & Brown (1981), but no classification showing relationships above the species level is used. Nonetheless, interspersed into many of the species accounts are notes that titillate the "I want to see this species in the field" juices of somebody like myself, especially since many of the butterflies are endemic to Hispaniola and of biogeographical interest. The discussion provides an ecological characterization of the entire butterfly fauna, and the genus *Calisto* is used as a model sounding board for the author's ideas on the evolutionary history of the entire area treated. My only complaint about the discussion is that I had trouble with some of the author's ecological terms (e.g., quasi-cloud forest, pseudoforest, p. 504; euryxenophiles, stenoxerophiles, eurymesophilic, stenomesophilic p. 505).

The person who wants an aesthetically pleasing reference on general butterfly biology, or who wants the book simply to identify butterflies of Hispaniola may find this book disappointing. In a modern treatment one expects to see illustrations of the butterflies for convenient identification. Instead of identification plates there is a decidedly onerous key; 24 pages in English, and then again in 24 pages in Spanish. The key is brimming with couplets like: "15. UP pale gray with darker gray to blackish markings... P. oileus; 15′. Not so...16; 16. UP orange...17; 17′. Not so...23 (p. 538). Regardless of what keys that have crossed my field of vision, I am always mystified by what "Not so" or similar statements mean. Perhaps because in my experience just about everything falls into these categories. The stoic who enjoys wrestling with the mysteries of keys may grin at my admission of sophomoric ineptitude with this key. However, nowhere in the book are we told how to separate the butterflies into families or genera — one must wade through every single couplet hunting a name for the specimen in hand. In short, I found the only means of identification in this book to be undiluted chloroform in print.

Surely Hispaniolan butterflies are more than a chunks of dead matter with vaguely described color patterns. I think the 15 black and white photographs of habitats (which are poor) should have been replaced with illustrations of butterflies. With a minimum of 13 specimens per plate, the keys could be eliminated and replaced with a line in the text on how to tell similar species apart, and the reader could easily identify the butterflies — even the 25 species of *Calisto* described by Schwartz and colleagues that are not illustrated in Riley (1975) or Brown & Heineman (1972). Perhaps the author and the publisher might wish to consider adding a set of plates to be sold with the book.

The lack of information on early stages and general references to butterfly natural history was disheartening. After acknowledging how few life histories of Hispaniolan butterflies are known, Schwartz states, "But intensive research

on caterpillars is not for visiting biologists; such work must be carried out by resident scientists (p. 2)". However, no attempt is made to help the reader into the literature, or even give the known hostplants in the species accounts. For a reference work I am puzzled why no reference to Vane-Wright & Ackery (1984), Ackery & Vane-Wright (1984), Scott (1986) is made in the literature cited — literature of decided importance to the butterfly fauna of Hispaniola.

To make use of this book, copies of Brown & Heineman (1972) and the out of print Riley (1975) should be kept near at hand. This will allow the reader to consult the plates and broader information content provided in the latter works. To potential buyers I recommend going to the local library and examining a copy of *Butterflies of Hispaniola* firsthand, then compare it to Riley's (1975) *Butterflies of the West Indies*, or Brown & Heineman's (1972) *Butterflies of Jamaica*. Dollars is not much money for a hardcover book, but I cannot honestly recommend this book to anyone except those who are already experts on Hispaniolan butterflies.

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INSTRUCTIONS TO AUTHORS

Manuscript Format: Two copies *must* be submitted (xeroxed or carbon papered), double-spaced, typed, with wide margins. Number all pages consecutively and put author's name at top right corner of each page. Underline all words where italics are intended. Footnotes, although discouraged, must be typed on a separate sheet. Do not hyphenate words at the right margin. All **measurements** must be metric. Metric altitudes and distances should include imperial equivalents in parenthesis. **Time** must be cited on a 24-hour basis, standard time. Abbreviations must follow common usage. **Dates** should be cited as example: 4. IV. 1979 (day-arabic numeral; month-Roman numeral; year-arabic numeral). Numerals must be used before measurements (5mm) or otherwise up to number ten e.g. (nine butterflies, 12 moths).

Title Page: All papers must have the title, author's name, author's address, and any titular reference and institutional approval reference, all on a separate title page. A **family citation must** be given in parenthesis (Lepidoptera: Hesperiidae) for referencing.

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Name Citations and Systematic Works: The first mention of any organism should include the full scientific name with unabbreviated author and year of description. New descriptions should conform to the format: description of male and/or female, type data, diagnosis, distribution, discussion. There **must** be conformity to the current International Code of Zoological Nomenclature. We strongly urge deposition of types in major museums, all type depositories must be cited.

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This index includes many articles of general interest which would not be found in the taxa or regional indices. Articles included are bibliographies, book reviews and opinions as well as topics of special interest such as aberrants and gynandromorphs as well as genetics and general laboratory techniques. All articles describing new taxa are also included. The subjects have been grouped into rather broad headings to eliminate cross-referencing. Only a small portion of the articles are included in this index. Again, we suggest that you refer to the author index for additional articles of interest.

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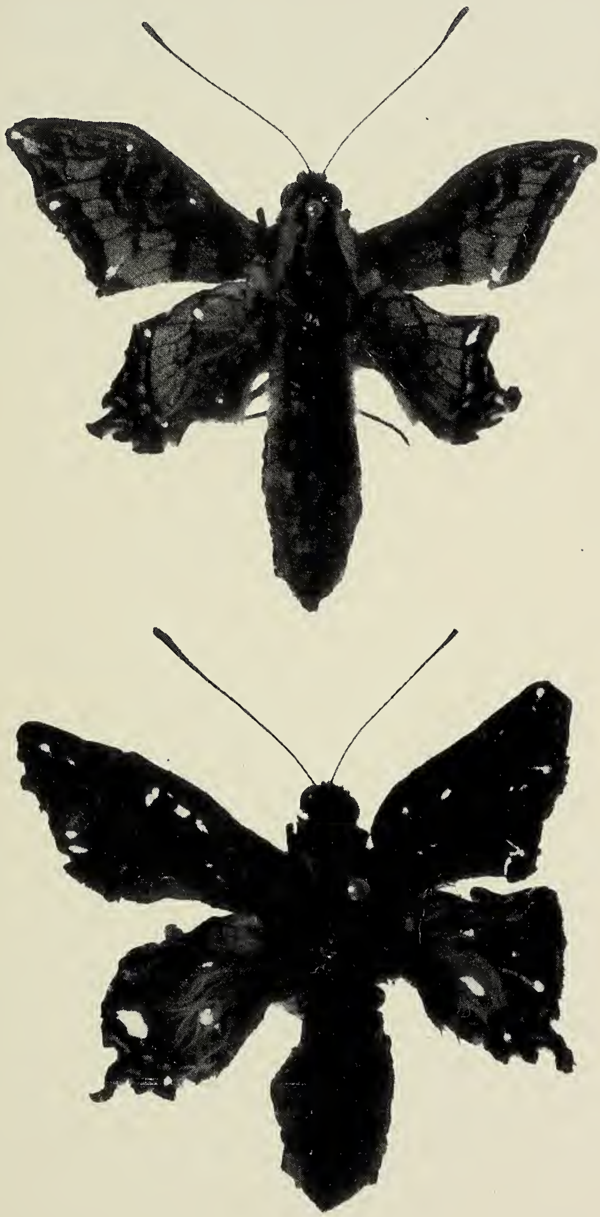

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Mating Behavior and Male Investment in *Euphydryas anicia* (Lepidoptera: Nymphalidae)

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and
Frank R. Stermitz[3]

Abstract. The size of male ejaculates in butterflies have often been suggested to play a key role in shaping the characteristics of butterfly mating systems. Females might choose males with larger ejaculates (greater nutrient investment), but a large ejaculate may be more costly for the male to produce. It remains unclear how various factors may interact to determine the size of male ejaculates. Rutowski (1984) called for tests over a range of species, including ones with unusually large or small nutrient investments. We studied mating behavior in *Euphydryas anicia*, which has an unusually small spermatophore (<2% of body weight), and suggest that spermatophore size relates strongly to many aspects of the mating system: male and female choosiness, female mating frequency, and the length and complexity of courtship.

Introduction

In some butterflies males transfer sperm and nutrients through mating to females (eg. Boggs and Gilbert 1979, Engebretson and Mason 1980, Walker 1980, Boggs 1981, Boggs and Watt 1981). A range of sizes exists for male ejaculates among species (Rutowski et al. 1983), and it has been suggested by many authors (for review, see Thornhill and Alcock 1983) that the size of the male nutrient investment plays a key role in shaping the characteristics of the mating system. Females would presumably perfer males with larger nutrient investments. Rutowski (1984) cautions that "untested assumptions underlie this conclusion" and that "students of the mating behavior of butterflies and moths should pay special attention to species whose males...produce [un]-usually large or small nutrient investments". One major untested assumption, for instance, is that offspring benefit from the nutrients transferred at mating. In studies on a moth (Greenfield 1982) and a butterfly (Jones et al. 1986), it was found that female fecundity was in

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fact not a function of the size of male ejaculate weight. Without a positive correlation between male ejaculate size and female fecundity, it is difficult to argue that males with larger spermatophores are more attractive to females.

Male ejaculate size may also affect the mating system through male choice. Recent evidence suggests that males incur non-trivial costs in producing ejaculates, that the number of ejaculates they can produce is limited, and therefore some discrimination should be expected with respect to their patterns of allocating ejaculates (eg. Marshall 1982, Dewsbury 1982, Svard 1985, Svard and Wilklund 1986). Rutowski (1985) studied choice in *Colias eurytheme* males which pass about 6% of their body weight (cf. Rutowski et al. 1983) to females at mating, and found that the size of females accepted by males is less variable than that of rejected females, implying choice by males. We studied the behavior of a butterfly with a very small spermatophore (<2% of male body weight), *Euphydryas anicia*. By following individual *Euphydryas anicia* in the field we were able to collect data on mate location behavior, mate discrimination, and courtship complexity and duration. Dissection of mated females gave information on spermatophore size and mating frequency. Our results support the prediction by Svard (1985) that males of monandrous species will tend to have small spermatophores, and may be compatible with those of Rutowski (1985) because of the difference in the size of the investment by the males of the two species studied. Like Rutowski's study, ours may support the notion that the size of the investment may be reflected in the degree of male choosiness. We discuss possible reasons for the small spermatophore in *E. anicia*, and discuss how a small spermatophore relates to other characteristics of the mating system.

Materials and Methods

Euphydryas anicia Doubleday and Hewitson occurs in scattered populations over the western half of the United States (White 1979, Cullenward et al. 1979, Ferris and Brown 1981). Near Red Hill Pass, 11 km east of Fairplay, Park County, Colorado, a population occurs in a part of a very flat, high altitude (2,900 m) intermontane plain (Odendaal et al. 1988). This site is an approximately 700 × 1300 m area containing a relatively localized population of *E. anicia*. The flight season is very short. Several years of site observations show that after snow has melted (early to mid-May) postdiapause larave feed on *Besseya plantaginea* and *Castilleja integra* (Scrophulariaceae), pupate, and emerge as adult butterflies in mid-June. About four to five weeks pass from first emergence to the last butterfly. For the first several days there are only males as occurs with other *Euphydryas* (Iwasa et al. 1983). Butterflies from this site contain bitter iridoid glucosides sequested during larval consumption of the host plants (Stermitz et al. 1986, Gardner and Stermitz 1988). Host and nectar plants are distributed throughout the site, although patchily in some years. All plants on the site are low-growing and herbaceous, with consequent excellent visibility for observing and censusing larvae, pupae and adult butterflies. During the 1985 flight season we conducted a mark-release-recapture program, capturing and marking 1260

males and 671 females. The first males were observed on June 13 and the first females on June 17, with an approximate 50:50 ratio reached on June 27. Behavior was observed during the entire flight season and some additional observations were conducted during the 1986 season.

MALE MATING BEHAVIOR

Individual field-collected males were marked and followed by two researchers, one recording behavioral events with a hand-held Radio Shack TRS 80 computer while the other marked landing spots. Males were recorded as collecting nectar, sitting, flying and chasing virgin females, previously mated (plugged) females, other males or other species.

FEMALE MATING BEHAVIOR

Because lab-rearing or tethering virgins may alter their behavior (Odendaal, unpublished data; M. Singer, personal communication), we followed unrestrained field-hatched virgins. Thirty-one virgins were encountered flying or just emerging from pupae in the field. Some were followed immediately, others were caught and released later the same day, while still others were kept for up to two days in a cage and fed with a mixture of honey and water (see Jones et al. 1986). One or two observers followed each virgin, noting and timing each type of behavior, and marking each landing spot with a numbered flag when possible. As a measure of relative local male density at various landing spots, all males passing within 1.5 m of a sitting virgin were counted. The same procedure was repeated with twelve field-collected plugged females.

Behavioral data for females were analyzed with an ANOVA to show whether a significant amount of variance in each of the parameters (flight frequency, average flight distance, local male density, number of male chases and chase distance) could be explained by female type (previously mated or plugged females, virgins that mated as a result of a male chase, and virgins that did not mate). Fischer's Least Significant Difference Test was performed for each parameter to determine whether the means of the female types differed significantly from one another.

SPERMATOPHORE DATA

Virgins that were mated were dissected within several hours of mating to obtain spermatophores, or were kept in a refrigerator, until dissection a few days later. Refrigeration slows down absorption of the spermatophore (C. Boggs, personal communication), and a truer assessment of the original spermatophore condition and weight is obtained. Forty-two field collected females were dissected for comparison. Spermatophores were described as full, half full and empty (when only a crust remained). Excised spermatophores and butterflies were dried at ambient lab temperature and low humidity. Our data using dry weight spermatophore to dry weight butterfly comparisons correlate extremely well with recent data for *E. editha* and *E. chalcedona* (Jones et al. 1986), where wet weight comparisons were used, presumably because both spermatophores and butterflies are approximately 75-85% water. The use of wet weights was suggested (Rutowski et al. 1983) to be of value since water has been considered a "nutrient" for female eggs (Marshall 1982b). This is not likely for *Euphydryas* species where water contributed from the spermatophore would represent an

insignificant portion of that present in the egg and where water has been shown to play no direct role in enhancing fitness in females (Murphy et al. 1983).

SIZE AND AGE OF INDIVIDUALS

The length of the forewing was used a size measurement. Wing wear, as an estimate of age, was determined for all females using a five point rating system (1 = extremely fresh, 2 = fresh, 3 = medium, 4 = old or worn, 5 = extremely worn; see Iwasa et al. 1983). Wing length and wear estimates were also obtained for males from field-captured mating pairs, and for 35 field-caught males.

WEATHER DATA

The condition of the weather was recorded about every fifteen minutes, or whenever it changed, by using the simple denotations *fair* (sunny, with little or no wind), *marginal* (largely cloudy with little sun or windy) and *bad* (heavy clouds or very windy). At least some butterflies were active during all three weather classes. When the weather became very bad, such as when wind was extremely strong or it was raining, no butterflies were active, and few were ever active if the sun was obscured for any length of time.

Results

MALE BEHAVIOR (Table 1)

Males tend to chase all flying objects vaguely the size of a *Euphydryas* butterfly, including other insects such as grasshoppers (for male behavior see also Odendaal et al. 1988, 1989). Males often chase other males, engaging in frantic erratic flights during which the original object of the chase is often replaced by another. Some of these flights included mating attempts. One extreme male-male chase lasted 22 minutes and involved numerous mating attempts, during which the pursuing role often switched and brief copulations were achieved three times.
From a total of 119 male chases recorded (Table 1), virgins were found to be chased longer than plugged females ($p<.005$, Mann-Whitney U-test), and plugged females were chased longer than males ($t = -2.4488$, $p<0.02$, Mann-Whitney U-test for large sample sizes see Siegel 1956); males were not chased significantly longer than other species ($t = 1.5088$, $0.1<p<0.2$, Mann-Whitney U-test). The extreme 22 minute male-male chase was not included in these data as males often switched pursuing roles, which made it difficult to time individual chases.

Males responded readily only to flying objects. They often flew within centimeters of sitting virgins or plugged females or even walked around on the same inflorescence with such females without reacting to them. Only when the female took flight would the male chase her.

FEMALE BEHAVIOR (Table 2)

Virgins that mated—Twelve of the 31 virgins mated in an average of 31 minutes after release. Of these, nine mated after an aerial pursuit by a male. In a typical case of these nine, a virgin sat for a while on a plant

Table 1. Summary of the duration of different types of male chases: males chasing non-specifics, males chasing males, males chasing females, and males chasing virgins.

Object of male chase:	heterospecific	male	mated female	virgin female
n	60	51	25	2
ave(sec)	2.86	3.72	11.96	98
S.D.	2.41	3.63	12.18	26.87

Table 2. Behavior data for females and ANOVA showing whether a significant amount of the variance in each of the parameters can be explained by female type. Asterisked entries have means that do not differ significantly (at.05 level) according to the Fisher's Least Significant Difference Test. Male density = Number of males passing within 1.5 m of a female per minute.

Behavior Parameters	FEMALES TYPE					
	Plugged Females (n = 12)	Virgins that Mated (n = 12)	Virgins not Mated (n = 19)	F	df	P
Flights per hour	15.50* ± 9.99	14.17* ±16.42	2.79 ± 3.31	4.02	2,35	ns
Flight Distance(m)	20.91* ±16.20	14.91* ± 9.64	12.00* ±13.59	4.83	2,25	ns
Male density	1.12 ± 1.98	9.52* ± 9.86	10.23* ± 7.73	7.15	2,35	p<.01
Male chases/min	0.83* ± 1.03	0.83* ± 0.58		0.00	1,22	ns
Chase Distance(m)	5.30* ± 8.87	20.20* ±21.01		4.27	1,18	ns

or on the ground and then made a short flight. Almost immediately a male gave chase. They landed, he crawled behind her, bent his abdomen, and they mated, achieving the straight back-to-back position within one minute of landing. Of the remaining three virgins, one was crawling on the ground, a second was collecting nectar and the third was hardening her wings after eclosion when mated. In these cases males landed virtually on top of the females, seemingly by accident. All virgins were mated by the first male that attempted mating and only one seemed to resist briefly by walking away a few centimeters prior to being mated.

During the 1986 season, two additional females were observed from eclosion to mating. Both had wings that had not hardened yet and were

sitting a few centimeters above empty pupal cases when encountered in the field. One mated 98 minutes and the other 101 minutes after observation began. In the first case, 68 males passed within 1.5 m and several less than ten cm from the virgin without reacting to her. Finally one male landed virtually on top of the female and they mated immediately. In the second case, 105s male passed within 1.5 m. Four short flights of less than 20 cm each were taken when no males were present, followed by a 10 m flight, during which one male and then a second chased her. She alighted and both males attempted to mate her, with one succeeding after about one minute.

As an additional measure of female choice we recorded wing size and condition of males. These factors did not differ significantly between 12 males that mated and 210 males collected during the same period (size: $t = 1.9178$, $p<0.05$; condition: $t = 0.6723$, $p<0.05$).

Virgins that did not mate—Nineteen out of 31 virgins did not mate during the time of observation (approximate one hour cut-off, usually due to unfavorable weather). Sixteen of these were never chased by males. Those that flew did so significantly less often and for shorter distances than virgins that mated (Table 2). Seven did not fly at all as opposed to only one of those that mated. Three virgins were lost from observation while being chased by males. One was pursued simultaneously by four males who also scrambled trying to mate with one another during the chase. The number of males that passed within 1.5 m of the virgins (relative male density) did not differ significantly between virgins that mated and those that did not (Table 2). In the cases of five non-mated virgins, males literally crawled over them or were side-by-side while obtaining nectar.

Previously mated (plugged) females—Plugged females flew greater distances and more frequently than virgins, but this was significant only in comparison with virgins that did not mate (Table 2). When pursued by males in flight, plugged females continue flying, trying to evade the males. If unsuccessful, they land and energetically flutter their wings during mating attempts. Six of the 12 plugged females were chased by males, two of them twice and one three times. None mated. (This nonreceptivity was observed many additional times during the 1986 season when we followed thirty-one plugged females in a detailed study of their behaviour and movement; see Odendaal et al., 1989. Plugged females fly differently from virgins. Once they have begun laying eggs, their abdomens become noticeably slimmer and their flight is smoother and stronger. Male density around plugged females was significantly less than around virgins ($p<.01$), but males chased both groups equally readily.

Spermatophore weights and condition (Table 3)—All twelve freshly mated females were dissected and classified as having full spermatophores. Dissection of 42 plugged females of various ages collected in the field over the season yielded only three that had mated twice, each

having two spermatophores. Of the 39 females that mated once, five had very old, shriveled spermatophores and near-empty bursas, whereas the remaining 34 had full or half full spermatophores. Of the three twice-mated females, two had one old and one fresher spermatophore and the third had two freshly deposited spermatophores. The ages of the three twice-mated females (x = 2.33) did not differ significantly from that of the 39 females (x = 2.76) that mated only once ($t = 0.5617$, $p<0.5$, Mann-Whitney U-test for large sample sizes; see Siegel 1956).

Virgins had a condition of 1 which differed significantly from the average condition of 2.69 of field caught females ($t = 6.1984$, $p<0.001$). Female body weight also differed significantly between the two groups ($t = 4.0572$, $p<0.001$), and body weight regressed significantly on condition (age), $F = 49.8804$, $p<0.001$. Spermatophore weight or % dry weight did not differ between the groups, and neither variable regressed significantly on condition (age).

A group of 43 field collected males were dried and weighed, with average weight being 27.7±5.1 mg. The range was 16.2 to 38.0 mg. The average spermatophore weight (Table 3) thus represents about 2% of the male body weight.

Effect of weather—The weather had a profound effect on behavior. When it was raining, or cold and cloudy, no butterflies were active. Butterflies were clinging to plants when it was too cold or windy to fly and could easily be picked up by observers. A few butterflies still showed sporadic activity when we classified weather as bad, and more when we considered the weather as marginal. We estimated about 56 percent of all potentially available time (daylight hours) to be good, about 29 percent to be marginal, about 3 percent to be bad, and about 12 percent of the time as too bad for any activity at all. To illustrate the effect of

Table 3. Summary of spermatophore data that were obtained from dissections of field-caught plugged females and lab-mated virgins.

		Age (days)	Body Weight (mg)	Spermatophore Weight (mg)	% Dry Weight
Field-caught females (n=42)	x	2.69	36.3	0.48	1.3
	S.D.	0.84	9.5	0.28	0.83
Lab-mated virgins (n=12)	x	1	48.8	0.64	1.3
	S.D.	0	9.2	0.37	0.66
t-value			-4.0572	-1.6501	0.010795
Significance level			1.6700^{-1}	0.01049 ns	0.9144 ns

slight weather changes on male butterfly activity, we plotted the number of male butterflies chasing females, other males or non-specifics/unit time for good and marginal weather (Figure 1).

Discussion

There remains a "specific lack of field data to understand the selective advantages behind the evolution and maintenance of large nutritive spermatophores" (Wickler 1986). This study shows that spermatophores in Colorado *Euphydryas anicia* are very small compared to those species investigated by Rutowski et al. (1983). What are the possible reasons for the small spermatophore size in this species?

Svard (1985) showed that male *Pararge aegeria* invested only about 1.4% of their weight under laboratory conditions, and explained this in terms of *P. aegeria* being a monandrous species with the male supplying only enough sperm to fertilize all the eggs of the female. The problem with this hypothesis is that the males in that study still produced 74% of material other than sperm. However, our data on female mating frequency do support the Svard explanation in that females in our field

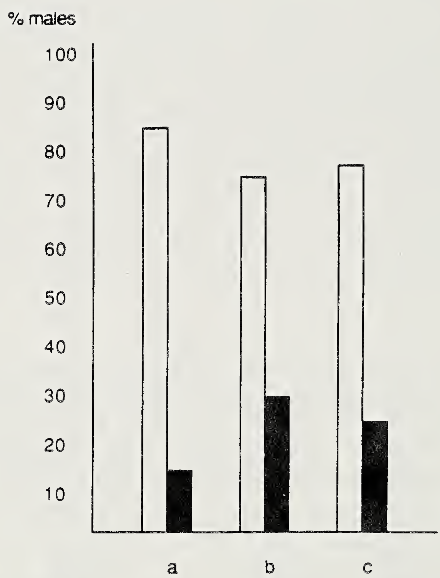

Fig. 1 Comparison of male behavior in good and marginal weather. Thirty-three *Euphydryas* males were followed in good weather for a total of 527 minutes and fifteen males in marginal weather for a total of 520 minutes. It was recorded whether they chased or ignored other males, females, and non-specifics that flew within a radius of 1.5 m past them. Clear bars indicate percentage of (a) other males, (b) females, and (c) non-specifics that were chased in good weather and solid bars percentage of passerby butterflies chased in marginal weather.

study showed a very low degree of polyandry (cf. Ehrlich and Ehrlich 1978).

The length of the breeding season may be one link between the environment and mating system characteristics (Odendaal et al. 1985a). In species with very short breeding seasons, females may be limited by the availability of time for repeated matings, host plant search and oviposition and should produce eggs mainly from resources acquired during the larval stage. The general picture in *Euphydryas*, which has a short breeding season (Iwasa et al. 1983), appears to support this. Singer and Ehrlich (1979) showed that only the offspring of the first egg batches have time to reach diapause in California *E. editha* before host plants senesce, and Murphy et al. (1983) showed that nutrient substances ingested by adults only slightly benefit later egg batches. Furthermore, Jones et al (1986) showed that the size of the male investment does not affect female reproductive output in *E. editha*. In contrast, female *Colias* butterflies did show reduced reproductive output with reduced male investment (Rutowski et al. 1987). On a high altitude plain in Colorado, time for locating and choosing host plants may be even more limited for *E. anicia* than for California *Euphydryas* because of lower temperatures and the frequently unfavorable mountain weather. Monandry may be advantageous. Male mating success is largely determined by access to fertilizable females (cf. Iwasa et al. 1983, Odendaal et al. 1985a) and if females tend to be monandrous, rapid mate acquisition may be crucially important to males. Viewed in this background, several points emerged from this study that may be related to a small male ejaculate:

(1) *Low level of mate discrimination for males and females*—Very limited time for locating and choosing host plants may have led to monandry in *Euphydryas* females. Females on this site use considerable time locating hostplants, then sometimes as much as an hour inspecting various plants and up to another hour laying eggs. This process is often interrupted by unfavorable weather. Monandry and a low level of female discrimination will place a high premium on rapid mate acquisition by males which may lead to a low level of male discrimination. Male *E. anicia* pursue any flying object that might possible be a conspecific female. Males also chase and try mating with one another. That these are true mating attempts is corroborated by the observation of brief amplexes between males. Males generally do not approach sitting males, females or even virgin butterflies but chase almost any insect that flies, presumably to maximize their chances of encountering fertilizable females. The data indicate that males follow virgins more persistently than plugged females, which in turn are followed more persistently than males. Odendaal et al. (1985b) suggested that there may be a close contact pheromone for identification of sexual partners, but since males also try to mate with males and plugged females it is

highly unlikely that males would discriminate among individual virgins in the field.

Similarly, females of *E. anicia* can hardly be regarded as discriminatory. All twelve virgins in 1985 and the two observed in 1986 accepted the first male almost immediately. These males were not larger than average. Rutowski (1984) builds a strong case for mate choice in the lepidoptera on the basis of nutrients passed from males to females in many species (eg., Boggs 1981; Rutowski 1982; Marshall 1982b). Females should select among males on the basis of traits (such as size) which indicate that they can provide a large nutrient investment (Thornhill 1976). This apparently is not true of *E. anicia*, presumably because of the small spermatophore produced by males, or because females acquired sufficient nutrients for egg production while in the larval stage (cf. Murphy et al. 1983). Jones et al. 1986 showed no relation between spermatophore size and reproductive output in *Euphydryas editha* and *E. chalcedona*.

(2) *Males exhibit scramble competition*—Time-constrained males of explosive breeders evaluate the quality of mates quickly if at all, and sometimes males seem unable to discriminate visually between males and females (Odendaal et al. 1985a). In four of the twelve virgins we observed mating, more than one male followed the virgin, and in three cases males scrambled intensely for her. One of the virgins we lost escaped when four males who followed her scrambled and tried to mate with one another. In 1986 we observed eight or nine males scrambling for a single virgin. Similar frenzied mating attempts were also observed with caged males (Odendall and Ehrlich, unpublished data).

(3) *Spermatophore size and female mating frequency*—As predicted by Svard (1985) for monandrous species, *E. anicia* spermatophores are very small relative to their body size. They are smaller than any recorded in the available literature (Rutowski et al., 1983). Females of the study population also remated very infrequently, with only three (7%) of field-caught females having more than one spermatophore. Furthermore, one of these females contained two fresh spermatophores and this could have been the result of scramble competition rather than a female tendency to remate. In a laboratory experiment Odendaal (unpublished data) once observed a virgin copulating with two males. Males often try to displace a mating male, and this may result in two spermatophores as the plug of the first one may not have hardened yet (Labine 1964). Percentage of the body weight made up by spermatophores did not differ between randomly collected mated females and freshly mated females, suggesting that females did not gradually use substantial amounts of the spermatophore for nutrition.

(4) *Length and complexity of courtship*—Rutowski (1984) states that nutrient investment made by male butterflies appears to have given rise to selection pressures that have shaped courtship behavior of males and perhaps females. Supportive data comes primarily from pierids (see

Rutowski 1984). Because of the small male investment in *E. anicia*, it may not be surprising that courtship is essentially non-existent in this population. All copulations were closely observed, sometimes from less than a meter away, and a successful mating merely involved the curling of the male's abdomen, sometimes a second or two searching for the female genital aperture with his genitalia, and copulation, which we regarded as complete when the couple achieved the straight back-to-back position. A further twenty copulations of caged butterflies obtained from this site and filmed on video tape yielded essentially the same results (Odendaal and Ehrlich, unpublished data).

Our work deviates somewhat from data on the *Euphydryas* species. The female remating frequency at Red Hill was considerably less than that for *E. editha* in California (Labine 1964) and there was a striking difference between relative spermatophore weights in the present work (<2%) as compared to that reported (10.8%) for three *E. chalcedona* individuals in Arizone (Rutowski et al., 1983). A detailed comparison of mating behavior of species within the genus *Euphydryas* would provide an interesting test of predictions on how spermatophore size may affect mating systems.

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The Biology of *Colias blameyi*(Pieridae), the "Green Sulphur" of the Argentine *Puna*

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Abstract. *Colias blameyi* Joergensen is a high-altitude endemic found in the *puna* of the Provinces of Catamarca, Tucumán, Salta and Jujuy in northwestern Argentina. It is probably double-brooded, with a seasonal up-and-downslope migration tracking the availability of its host plants, *Astragalus* spp. (Leguminosae). The early stages, reared on alfalfa (*Medicago sativa* L.) are described. The relationship of *C. blameyi* to other taxa of high-altitude Sulphurs in the central Andes remains problematical.

Introduction

The biogeography of the high-Andean butterfly fauna is receiving renewed attention in the context of attempts to reconstruct Quaternary climate dynamics and their impact on biotic diversity in tropical America (Brown 1987, Descimon 1986, Shapiro 1989). For most groups, both distributional and biological data are still inadequate for a proper analysis to be done. In many cases the sister-groups of endemic Andean taxa are unknown. The genus *Colias* has its greatest diversity in the Holarctic, but has undergone considerable adaptive radiation in the cold and temperate parts of South America. The systematic position of the Andean *Colias* is far from resolved. Descimon (1986) considers them a monophyletic group, while Berger (1986), in a global revision at the subgeneric level, does not. The characters used by Berger to delimit subgenera are superficial and poorly if at all rationalized, while Descimon's discussion is informal and his bases for judgment are inexplicit. Speculation must be replaced by data if progress is to occur. Descimon has reared several Andean *Colias* and indicates (*loc. cit.*) that their life-histories will be published. One which he has not reared is *Colias blameyi* Joergensen, whose life-history is reported here.

In 1916 Pedro Joergensen, one of the three founders of Argentine Lepidopterology (with Eugenio Giacomelli and Carlos Berg), published a landmark monograph on the Argentine Pieridae which included the description of a new *Colias* from the Sierra de Aconquija, Provinces of Catamarca and Tucumán. The Sierra de Aconquija and Cumbres Calchaquíes form a major eastern outlier of the Andes proper, reaching altitudes over 5000 m (Nevado del Candado, near the southern end of the Aconquija range, reaches 5450 m), and separated from the Andes by a deep trough, the Valles Calchaquíes. Moisture-bearing winds strike

the range from the east, so that there is a very pronounced rain shadow west of the crest. The seasonally wet climates east of the crest provide the last refuge for many humid-Neotropical biotic elements of the mid-elevation forest zone, while the subalpine and alpine zones shelter many elements of the central Andes (Peru, Bolivia) which drop out in the Andes themselves south of the Province of Salta. Joergensen was able to mount several expeditions into the Aconquija range with the help of his friend Joel Blamey of Huazán, after whom he named his new Sulphur. There was a burst of description of new Andean *Colias* around this time, but as usual they were published in European journals and Joergensen was unaware of them; for him the dusky green phenotype of *Colias blameyi* was something entirely new for the continent, and it immediately reminded him of various boreal Holarctic species: "The male of this new little species. . .cannot be confused with any of its South American congeners, but it has the size and the dark glaucous green ground color of the species *nastes* Boisduval and *behri* Edwards, the former from the North American Arctic (Labrador, Greenland, Alaska and British Columbia), the latter from the mountains of California; but the patterns are different." (Translation by A.M.S.) He provided an excellent, detailed description of both sexes and a brief summary of what he knew of its biology. Since then this striking insect has been collected occasionally by travelers, but nothing further on its biology has appeared. If Kenneth Hayward knew any more about it, his information apparently died with him, as the projected Pierid volume in Hayward's monograph of the Argentine butterflies never appeared and no manuscript has been found. Although several South American *Colias* have been reared, the only species for which published information on the life-history and early stages is available is *C. lesbia* Fabricius, which is a serious alfalfa pest in several countries. It has been monographed by Biezanko (1954), Freiberg (1947), and Reed (1922). Although *C. blameyi* is common in the proper habitat in season, specimens are rare in collections — even in Argentina itself.

Biology of Adults

Joergensen (1916, p.510) states that *C. blameyi* "is common on the summits of the grassy mountains: Cerro La Tambilla, 3700 m; Cerro Medio, 3750 m; Cerro Yutoyaco, 3500; Cerro Negro, 3500, and Cerro La Ensenada, 3200. All these localities are east and southeast of the snowy summits of the Aconquija range. There it flies from the end of January until the end of April. Its flight is not very high, but in good weather it seems constantly in motion, (though) often settling on the ground or on flowers such as *Gutierrezia repens* Gr., *Hypochaeris meyeniana* Wolp. (Compositae), *Verbena microphylla* H.B.K. (Verbenaceae), *Malvastrum capitatum* Gr, and *M. parnassifolium* Hook. (Malvaceae). When the hard freezes begin on the heights in late March, it descends. . .to more protected valleys, for example at La Ollada (3100 m), where it is never

found in summer." Joergensen was an excellent observer and is correct on all points.

There is no amplification of the range, as stated by Joergensen, in any subsequent literature. Because the closely related entity *C. weberbaueri* Strand, which differs from *c. blameyi* primarily in its lack of an androconial patch in the male, is the only taxon of the group recorded in Bolivia, it is important to note that *C. blameyi* is not confined to the Sierra de Aconquija. Within the Province of Tucumán it extends north an indeterminate distance well into the Cumbres Calchaquíes, which extend to the NE of Abra Infiernillo (3300 m), where Highway 307 (Monteros-Amaichá del Valle) crosses the range. In the true Andean *puna* it, or an entity transitional from it to *C. weberbaueri*, occurs abundantly in the Provinces of Jujuy (Abra Pampa, Tres Cruces, Esquinas Blancas, 3693-3875 m, all along Highway 9 above Humahuaca) and Salta (Cuesta del Obispo, Abra Molina, Cerro Zapallar, Valle Encantado, all along or near Highway 33). There is great individual and interpopulational variability in both sexes (figs. 1,2). *Puna* animals average lighter than Tucumán and Catamarca ones, but nearly all have well-developed androconial patches. There is no obvious tendency for them to be smaller, or more frequently reduced, in the *puna* than in the Aconquija-Cumbres Calchaquíes populations.

Both sexes fly from roughly 1000 to 1500 daily in good weather. Flight initiation in the morning occurs with air temperatures of roughly 10°C with light wind and strong sunshine. Flight may be terminated early by cloudiness or, even under clear sky, by strong and turbulent upslope afternoon winds which often develop on the eastern slopes of the Tucumán-Catamarca ranges and at the head of the Quebrada de Humahuaca. A few animals continue to fly in the lee of ridges or hills until the sun fails to reach them.

Males patrol linear habitats such as roadsides, streamsides and gullies, and below the crests of ridges, but do not hilltop. They can often be seen coursing back and forth over alpine grassland and rock gardens (as in fig.3) about 1 m above the ground. All-male aggregations occur on moist earth, at puddles and along streambanks. Up to 30 animals have been seen puddling together, mainly after 1330. Females occur singly and are seldom seen where males are patrolling. Most of my observations of females have been at or near summits, where host plants grow among rocks, or around shrubs, where they often grow within the drip line. Oviposition occurs singly, usually on the underside of a leaf, and females will frequently proceed in more or less of a straight line, laying one egg on each plant they encounter.

Host Plants

Three definite hosts have been identified (by R. Barneby, New York Botanic Garden). All are based on many (> 10) oviposition records/each.

They are *Astragalus garbancillo* Cav. and *A. micranthellus* Wedd., both at Tres Cruces, Jujuy, 3800 m±, and *A. hypsogenus* I.M. Johnston, at both the summit of Cerro Zapallar, ca. 4200 m, Salta, and on several summits near Abra Infiernillo, Tucumán, ca. 3500 m (all Leguminosae).

These three species are disparate in both facies and phylogenetic affinities. Their differences imply that *C. blameyi* is a generalist at least within the genus *Astragalus. Astragalus* is very well-developed and diverse in the Andes (Johnston 1947). *A. garbancillo* is "the most widely distributed and most commonly collected South American *Astragalus*" (Johnston 1947, p. 384). It is erect and ascending in habit. In Argentina it is largely confined to moist and dissected areas at the periphery of the *puna*. It is a common species in much of the range of *C. weberbaueri* in Bolivia and Peru and should be considered a probable host. It is taxonomically isolated within the genus *Astragalus*.

Astragalus micranthellus is depressed, prostrate to tufted and much less leafy and conspicuous than *A. garbancillo*. Its range includes *altiplano* and *puna* in Peru and Bolivia, extending in Argentina only as far south as the Sierra de Aconquija (Johnston, p. 391).

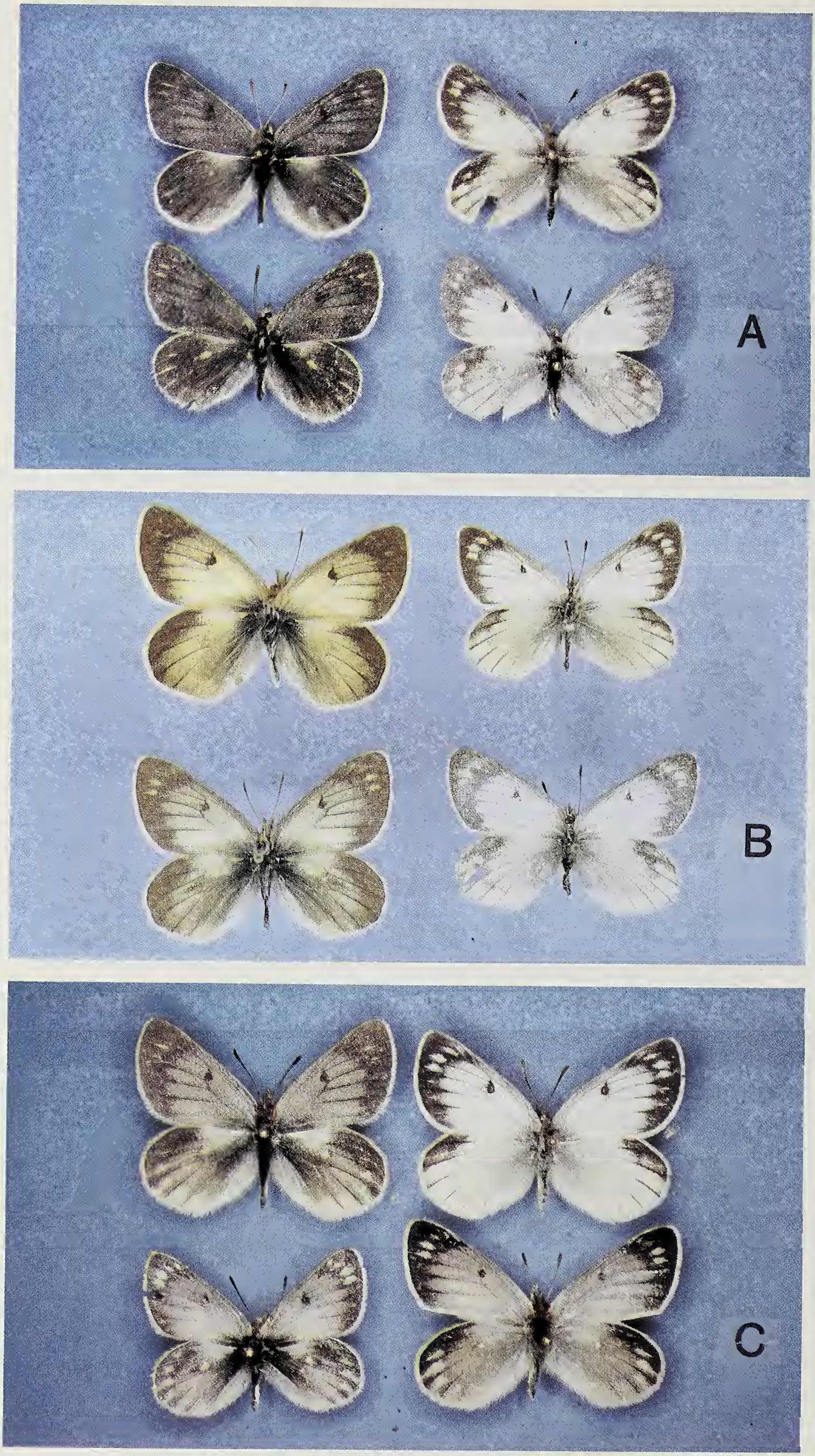
Astragalus hypsogenus is a small, tufted plant with tiny leaves but very showy purple flowers, reminiscent in habit of some of the alpine *Lupinus*. It is one of the aspect dominants of alpine rock garden habitats on the wetter summits in both Salta and the Aconquija-Cumbres Calchaquíes and grows in the sites shown in both figs. 3 and 4. Its range includes Bolivia and northern Argentina, again not south of the Sierra de Aconquija. It forms a compact, isolated species-group along with *A. confinis* I.M. Johnston and *A. crymophilus* I.M. Johnston.

Both *A. garbancillo* and *A. micranthellus* are confirmed wild hosts of the pierine *Tatochila distincta distincta* Joergensen, which can however be reared on Crucifers in the laboratory (Shapiro 1986). This butterfly co-occurs with *A. hypsogenus* in both Salta and Tucumán, as does the very rare and as yet unreared *T. inversa* Hayward.

Early Stages

No significant differences have been observed in material from Salta, Jujuy and Tucumán. Rearing was done at Davis on alfalfa (*Medicago*

Fig. 1. *Colias blameyi* from these disjunct populations in northwestern Argentina, males at left. A: Quebrada Carapunco, Province of Tucumán, 20.i.1986. B: Esquinas Blancas, Province of Jujuy, 7.ii.1984. C: Summit of Cerro Zapallar, Province of Salta, 22.i.1986. The Tucumán populations are essentially topotypical. The Salta and Jujuy populations resemble *C. weberbaueri* from Bolivia but have well-developed androconial patches in the males.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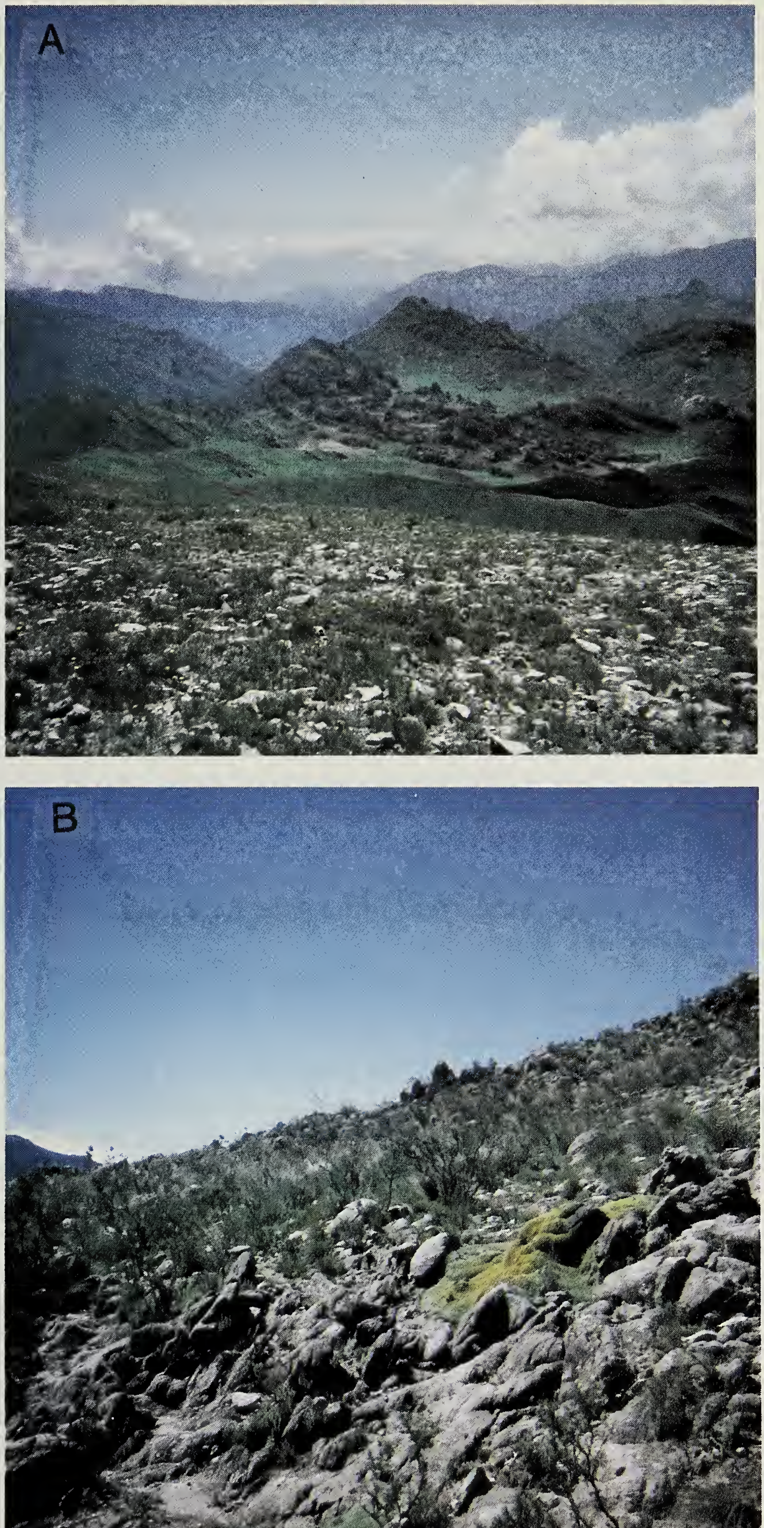
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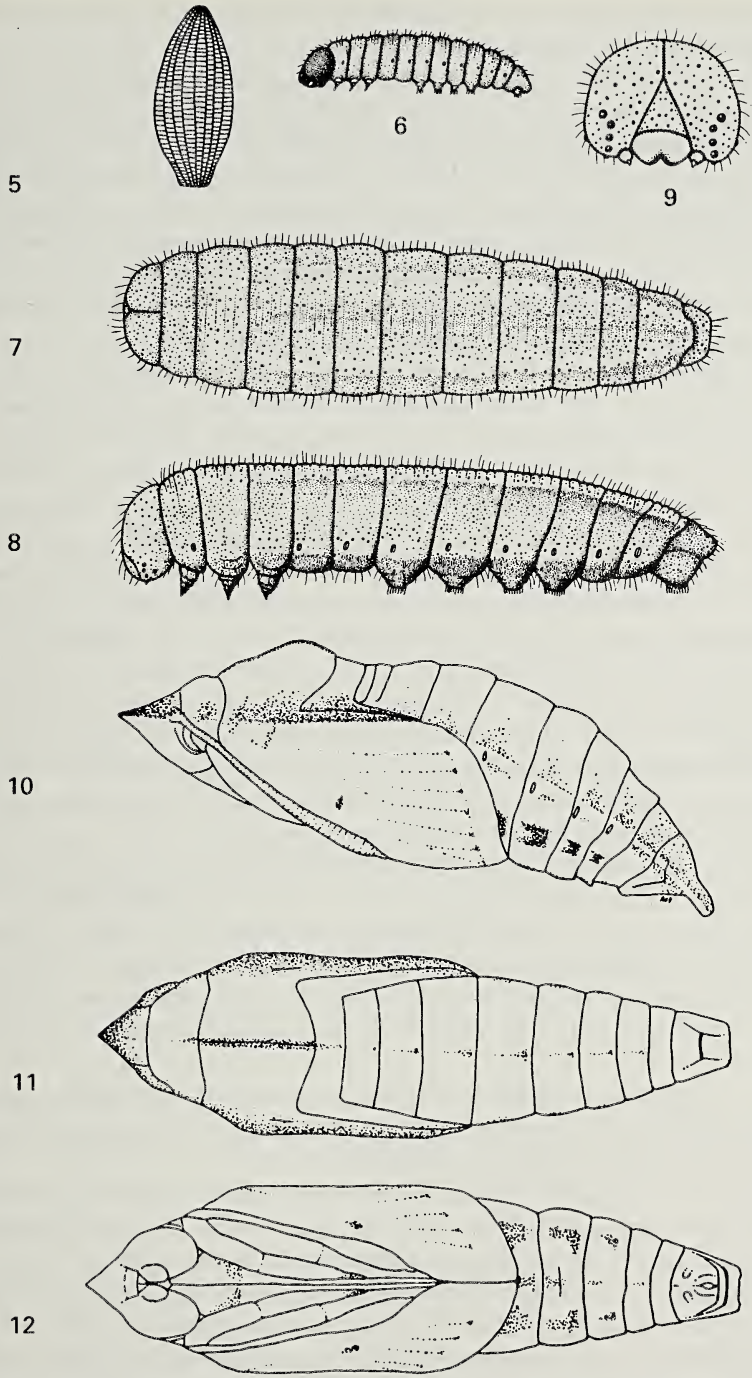
sativa L.) cuttings; *Vicia benghalensis* L. was eaten but no larvae survived beyond the third instar on it. Larvae were kept in plastic Petri dishes under 14L:10D, 23.9°/12.8°C. Preserved early stages have been retained at Davis. All color descriptions are from life. Those in parentheses refer to the color-standards system of Kornerup and Wanscher (1978).

Egg (fig. 5). — Erect, fusiform, strongly tapered at both ends, 1.1 × 0.3 mm, the chorion sculptured as figured with about 16-17 and 42-52 vertical and horizontal ribs. Madder red (9A7) when laid, becoming translucent about 12 hr before hatching. Laid singly, usually on lower leaf surfaces. Newly-hatched larvae do not eat their eggshells. Time to hatch, 7-8 days.

Larva: *First Instar* (fig. 6). — At hatch 1.15 mm, grayish to brownish orange, the head much darker; head and body with pale, mostly glandular hairs disposed as below. After feeding grayish green (1D7) dorsally, grayish yellow (1B3) ventrally, a darker shade immediately below the spiracles and above the prolegs, gradually lightening toward the venter. First thoracic segment with a transverse fold and 9-10 glandular hairs in a single row. Second and third segments with folds dividing them into five annulae, the fourth (counting caudad) bearing 8 glandular hairs in a single transverse row. First two abdominal segments each with four annulae, of which the first and fourth each bear two glandular hairs. Other abdominal segments with five annulae, the first and fifth of which each bear two glandular hairs, except the eighth and ninth with three annulae, two hairs each on first and third; and the last with a darkened sclerotized shield bearing several dark, non-glandular setae, plus six glandular hairs anterior to the shield. Excavates strips of parenchyma; feeds by day and night and rests along the midrib. Lenght of instar, 3-4 days.

Second Instar. — After molt 3.8 mm. Similar, with annulae disposed as follows: five annulae per segment except the following abdominal segments with six: second, fourth, fifth, seventh; third with seven; ninth and tenth apparently unitary. This arrangement is continued in later instars, with intercalation of annulae on some segments especially near the front of the abdomen. Dorsal and lateral surfaces densely covered with small dark tubercles in two sizes, each surmounted by either a

Fig. 2. Habitats of *C. blameyi* in wet season, during the flight period. A: Summit of Cerro Zapallar, Salta, looking toward Valle Encantado below. Both sexes are common here, flying over alpine rock gardens. B: Rocky summit at about 3900 m in the Cumbres Calchaquíes near Abra Infiernillo, Tucumán. Females occur here and oviposit on *Astragalus hypsogenus* among the rocks. The yellowish cushion plant is *Azorella* (Umbelliferae, "yareta"), a characteristic alpine plant in the region.



Figs. 5-12. Life history of *C. blameyi*. 5, egg; 6, first-instar larva, lateral view; 7, fifth-instar larva, dorsal view; 8, same, lateral view; 9, same, head capsule; 10, pupa, lateral view; 11, same, dorsal; 12, same, ventral.

glandular or a simple hair. Head darker than body, densely tuberculate. No change in habits. Duration, 3-4 days.

Third Instar. — After molt 5.25 mm. Similar, tubercles densely and rather evenly distributed over dorsal and lateral surfaces of body and even more densely on head, the larger ones darker and bearing mostly dark hairs, the smaller either darker or concolorous and bearing either dark or pale hairs. Head capsule scarcely darker than body: ocelli black. A vague pale line on each side incorporating the spiracles; directly below it a very dark shade of the ground color, grading insensibly into the paler venter. Third instars consume epidermis as well as parenchyma. Length of instar, 4-5 days.

Fourth Instar. — After molt 8.5 mm. Similar, with a decidedly granular appearance due to the very numerous tubercles and hairs. Rests lengthwise on the petiole when not feeding. Length of instar, 5 days.

Fifth Instar (figs. 7, 8, 9). – After molt 14 mm, reaching 23 mm at maturity. Head and body above olive (2E6) with numerous tubercles, both dark and concolorous, over the dorsal and lateral surfaces; hairs both light and dark, between 50-100 per annulus. Spiracles not contrasting, but incorporated in an ill-defined pale line (grayish yellow, 1B3) not enclosing any red or pink color; below this a darker shade of the ground color, passing into dull olive (2D4) just above the bases of the legs, which are concolorous with the venter. Crochets black. Dorsal midline slightly darker than ground; the entire dorsum slightly paler than the sides, the pale hue ending abruptly where the subdorsal pale stripes would be if present. Head dark olive, densely tuberculate, the tubercles bearing dark hairs; ocelli brownish-black.

The mature larva feeds by day and night in the lab, resting on stems. If disturbed, it drops to the ground in a coil, reascending the plant 10-15 min later. This is a stereotyped defensive reaction in all *Colias* I have reared. The day before pupation the larva turns grayish with a slightly purple tinge, leaves the plant and wanders for several hours before spinning a mat of silk in preparation for the molt. Duration of instar, 7-10 days.

Prepupa. — Formed vertically, head up, pendant by the silken girdle and attached at the cremaster, appearing greasy and grayish-yellow-green. Length of prepupal period 20-36 hr.

Pupa (figs. 10, 11, 12). — Typical *Colias* form, chunky, the wing-cases not particularly inflated and the frontal prominence short and broad; length 14-15 mm, width at base of abdomen 3.3-4 mm. Dorsal surface olive yellow (2C7); ventral, including wing cases, canary yellow (2B7). Proboscis not reaching tips of wing cases. Wings with a black dot corresponding to the discocellular spot of the adult and black dots at the vein-tips. Brownish-red (10C7) shading as follows: on dorsal surface of the frontal prominence; along hind margin of wing cases; on the dorsal thoracic keel; above the spiracles; and two parallel rows of blotches on the ventral abdomen, one on either side of the midline. Spiracles

enclosed in a yellowish-white, moderately contrasting line. Eyes, wings and body becoming pigmented in that order the day before eclosion, the wings of both sexes initially yellowish-white, those of the males subsequently turning dark (black pigment laid down several hr after white). First meconium dull rose pink, second colorless. Time to hatch, 12-17 days.

Diapause. — *Colias* usually diapause as third-instar larvae. Several larvae indeed stopped feeding in the third instar and survived 2-4 wk thereafter, but there was so much disease mortality that I cannot say with confidence that they were attempting to diapause. Altitudinal migration, such as between La Ollada and the Sierra de Aconquija or between Valle Encantado and the summit of Cerro Zapallar, may be a seasonal strategy to avoid severe cold and to track host plant availability. In many insects such migration substitutes for diapause as a mechanism to avoid seasonal stress. *Colias blameyi*, however, disappears altogether for more than half the year and diapause is thus very likely. Descimon (1986) echoes other authorities in recording the entire assemblage of pale and green *puna* species as flying only in rainy season ("March-April, or December in the Arequipa region").

Altitudinal migration appears to be very common in the butterfly fauna of the northwestern Argentine highlands. Several species of *Tatochila*, including *T. sterodice macrodice* Stgr., *T. stigmadice* Stgr. and *T. orthodice* Weymer, which fly with *C. blameyi* in January and February, can be found at much lower elevations in the Provinces of Salta and Tucumán in November. The member of the *Phulia nymphula* Blanchard complex (*aconquijae* Joerg.) found in the Aconquija and Cumbres Calchaquíes parallels *C. blameyi* in its winter retreat to the level of La Ollada.

Comparisons to C. lesbia. — *Colias lesbia* is larger (except in cold-weather broods) throughout its development, and both the larva and pupa are more slender. The disposition of annulae and glandular hairs on the first-instar larva is very similar, but the number of annulae diverges in later instars. The larva of *C. lesbia* is bright "alfalfa green" rather than dull or olivaceous green as in *C. blameyi*, and has a pink spiracular line. The pupa is brighter green and has a bolder spiracular line with silvery reflections. Both morphology and pattern are very conservative in *Colias* immatures, as noted by Descimon (1986). Until a detailed morphological study is done of representative members of various species-groups, isolated rearings will cast little light on the Holarctic sister-group of the Andean group to which *C. blameyi* belongs; the relevant information is still largely lacking for the Holarctic taxa as well. There is nothing in these descriptions which would lead one to question the joint membership of *C. lesbia* and *C. blameyi* in a monophyletic Andean group, but the point is moot until more descriptions are available. All of the Andean species reared so far are Legume feeders, though some are presently known only from naturalized European clovers.

Discussion

The group of taxa embracing *C. blameyi*; *C. weberbaueri*, *C. erika* Lamas, and *C. mossi* Rothschild (including "form" *nigerrima* Fassl), all from Peru; and *C. flaveola* from Chile (and northwestern Argentina, Shapiro, unpublished), is badly in need of revision. Of the heavily melanized taxa only *weberbaueri* is recorded in Bolivia, but *blameyi* is now recorded within about 25 km of the Argentine-Bolivian border in the *puna* of Jujuy, and *flaveola* is now known to cross the Andean crest and penetrate the eastern slope. Berger (1986) treats *blameyi* as a subspecies of *mossi* but *weberbaueri* becomes a separate species by virtue of its lack of an androconial patch. Descimon (1986, p. 506) states that this is a fluctuating character in some populations, even of *flaveola*. Shapiro (1985) has published a figure of a melanic aberration of *C. euxanthe stuebeli* Reiss. from the Department of Cusco, Peru. The type of melanization displayed is quite different from that of melanic aberration of the Nearctic *C. philodice* Godt. and *C. eurytheme* Bdv. but agrees perfectly with that seen in the *puna* complex, underscoring the point that phenotypic similarity within this group could easily have arisen by parallelism. It cannot be assumed automatically that all the "green" taxa are more closely related among themselves than they are to the non-"green" ones.

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The Early Stages of *Doa dora* Neumoegen and Dyar (Lepidoptera: Noctuoidea: Doidae) in Baja California, Mexico

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Abstract. The early stages of *Doa dora* Neumoegen and Dyar from Baja California, Mexico, are described and illustrated. Adults were reared on *Euphorbia misera* Bentham (Euphorbiaceae) from eggs deposited by females collected on Isla de Cedros. The unique combination of larval characters possessed by the doids, i.e., small head, hump-backed thorax, biordinal crochets in a homoideous mesoseries, and integumental spicules, contradict traditional assignments to families of similar adult morphology (i.e., Lymantriidae, Hypsidae, Pericopidae, Artiidae). It is likely that specimens from the northern part of the range of *D. dora* (i.e., Baja California and Sonora, Mexico) represent an undescribed species. Although adults have not been collected in the United States, larvae have been taken in San Diego, California.

Introduction

The genus *Doa* Neumoegen and Dyar (1894) has traditionally defied attempts at familial assignment. Its long history of taxonomic uncertainty includes placement in the Lymantriidae (Dyar 1903; Barnes and McDunnough 1917; Holland 1903; Bryk 1934), Hypsidae (Walton 1912), Pericopidae (Schaus 1927; McDunnough 1938; Peterson 1948), and Arctiidae (Franclemont 1983). Most recently, *Doa* and its sister genus, *Leuculodes* Dyar, have been treated as a distinct family — the Doidae (Donahue and Brown 1987). However, the phylogenetic relationship of *Doa* to other noctuoid families is uncertain, and elevation to family level probably represents only an interim solution. It is likely that the early stages will provide characters useful in illuminating relationships among the doids and other noctuoid clades.

Dyar (1911, 1912) provided superficial descriptions of the early stages of *Doa ampla* (Grote) and *Doa raspa* (Dyar). However, features of the chaetotaxy and crochet arrangement have been presented only recently (Donahue and Brown 1987). The purpose of this paper is to provide

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descriptions and illustrations of the larva, pupa, and adult, and notes on the biology of *Doa dora* Neumoegen and Dyar in Baja California, Mexico. It is not my intention to draw conclusions regarding the phylogenetic position of the Doidae, but to make available specific life history information that has accumulated.

Materials and Methods

A single female *Doa dora* was collected at blacklight (UV) on the north end of Isla de Cedros, Baja California, Mexico, 31 March 1983. A second female was collected the following morning, while it perched on a large bush of *Euphorbia misera* Bentham (Euphorbiaceae). On 2 April 1983, a fourth and a fifth instar larva were collected on *E. misera* by D. K. Faulkner, near El Pueblo, in the southeastern portion of the island.

The adult females were confined together in a plastic bag with a fresh cutting of *E. misera*. They readily oviposited on the leaves and stems of the plant material. I estimated that between 50 and 75 eggs had been deposited by the evening of 5 March. The eggs were taken to San Diego, California, where the larvae were reared to maturity on local *E. misera*. As the eggs hatched, larvae were transferred in small groups to 4.5 ounce glass jars with small pieces of netting for lids. When the larvae reached the third instar, they were transferred to a cylindrical, half-gallon, cardboard container, where they continued to feed and eventually pupated. Rearing was done indoors at ambient temperature (65–77°F).

Upon emergence, most adults were removed. However, the last 5 or 6 were left in the container. Mating took place within 1 to 3 days of eclosion; females readily oviposited on the dry plant material remaining in the container. A second generation was reared from these eggs. Insufficient host material resulted in a brood of dwarfed adults. All specimens are deposited in the collection of the San Diego Natural History Museum (SDNHM).

Description of Early Stages

Morphological terminology and homology of setae follow Stehr (1987); terminology and homology of pupal characters follow Mosher (1916).

Egg. Flattened, oblong, oval; width ca. 0.6 mm, length ca. 0.85 mm; chorion with fine punctations; light yellow when first laid, becoming conspicuously collapsed as embryo develops; becoming transparent 2–3 days prior to hatching, revealing gray larva, with dark gray or blue-gray spot representing head. *Last Instar Larva*. General (Fig. 1): Total length 18.0–22.0 mm. Head small, smooth, shiny, without secondary setae. Thorax inflated, larva appearing slightly humpbacked (although not as pronounced as in *Doa ampla*). Integument with dense

Fig. 1. Last instar of *Doa dora*

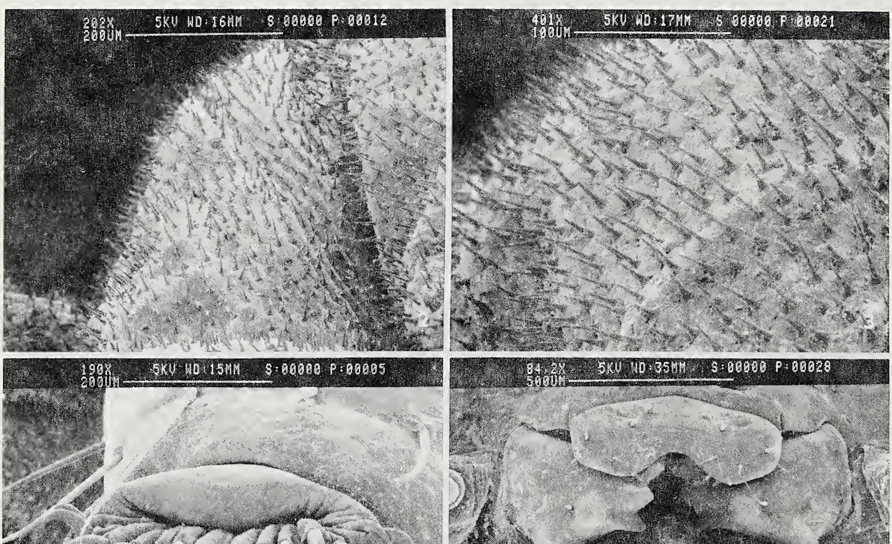

Fig. 2. Integument of last instar larva showing spicules.
Fig. 3. Integumental spicules at higher magnification.
Fig. 4. Crochets of abdominal proleg of segment VI.
Fig. 5. Mouthparts of last instar.

spicules (Figs. 2–3); all setae simple; pinacula small or absent. All prolegs equal in size; crochets biordinal, in homoideous mesoseries (covering approximately 0.60 perimeter of planta) (Fig. 4). Spiracles small, elliptical, peritreme well sclerotized, uniform in size on A1–A7, those on T1 and A8 larger.

Head: As in Figs. 5–7. Width 1.8–2.0 mm. Height of frons approximately 0.8 mm. Length of epicranial suture approximately 0.75 x height of frontoclypeus. Frontoclypeal height slightly greater than its basal width. P1 setae about twice as far apart as P2s, P2s located dorsad of juncture of adfrontal line; A2 dorsoanterad of A1; L1 nearly in a straight line with A1 and A2; L2 posteroventrad of L1. Six stemmata (Fig. 7), 1 and 6 similar in size, larger than 2–5; stemmata 1–4 nearly equally spaced in an arc; 5 and 6 approximately equidistant from 4. Seta S2 below stemma 1; S1 below stemma 6. Labrum with a broad, u-shaped, ventral notch. Mandible (Fig. 10) nearly square, with two lateral setae; inner surface with 3 triangular teeth.

Thorax: As in Fig. 8. Segment T1: Cervical gland absent; prothoracic shield greatly reduced, bearing only XD1 and XD2. D1s closer to meson than XD1s; XD2s slightly further apart than D2s; SD1 dorsad of spiracle; SD2 small, between XD2 and spiracle; L group bisetose, anterad and slightly ventrad of spiracle; SV group bisetose. Segments T2–T3: D2 closer to meson than D1; SD2 directly ventrad of D2; SD1 anteroventrad of SD2; L1 unisetose, in line with spiracles; L2 anteroventrad of L1; L3 dorsoposterad of L1, in nearly straight line with L2 and L1; an extra seta directly posterad of L2 and ventrad of L3; SV group bisetose. Legs: Femur with 2 mesal setae; tibia with 6 setae in ring around circumference; tarsus with 3 setae.

Abdomen: As in Fig. 8. Distance between D2s approximately 2 x distance between D1s. A1–8 with extra seta dorsad of D2, giving appearance of 4 (total) equally spaced D2 setae in transverse line across dorso-meson. SD1 dorsad of spiracle, SD2 greatly reduced. L1 unisetose, posterad of spiracle; L2 and L3 approximately halfway between spiracle and SV1, about one spiracle height apart, L3 slightly ventrad to L2. SV1 unisetose on A1–2 and A7–9, absent on A3–6. SV2 bi- or trisetose on A1–A6 (variable on opposite sides of same segment), unisetose on A7–9. SV3 unisetose on A1–2, absent on A3–9. A9 with D2, SD1, SD2, and L1 on nearly contiguous pinacula in a diagonal line. A10 (Fig. 9) with 20–24 setae irregularly arranged. Prolegs with 12–15 lateral setae; planta with 20–24 biordinal crochets in homoideous mesoseries.

Color: Head shiny brick red; a prominent black patch at stemmata; clypeus and bases of antennae white; labrum black. Body with a series of longitudinal stripes from meson to prolegs arranged as follows: black at middorsum, bordered by white, black, yellow, black, white, black, yellow with two black dots on each abdominal segment (anterior one larger, including spiracle), black, white with two black dots per

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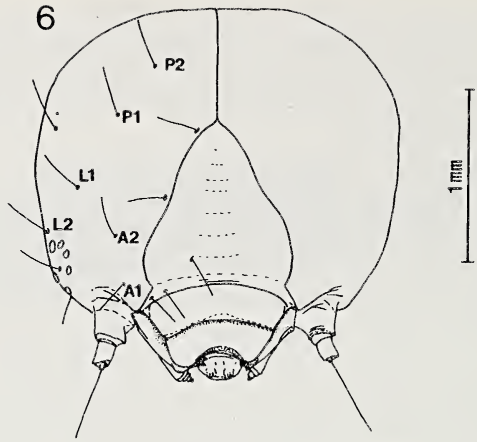

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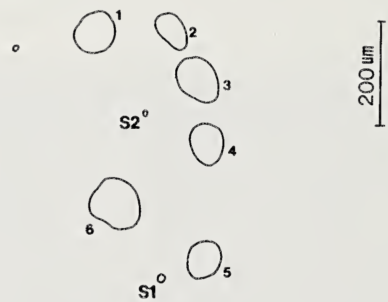

Fig. 6. Head of last instar; anterior view.
Fig. 7. Arrangement of stemmata; lateral view; anterior at right.

abdominal segment, black; A–10 brick red. Thoracic legs brick red; tarsi black. Entire dorsal surface smooth and rather shiny; ventral surface mostly black with diffuse yellow bands laterally between pairs of legs.

Although *D. dora* is most similar to *D. ampla* in both superficial facies and genital morphology, the larvae are remarkably different in coloration.

Pupa: As in Figs. 11–12. Total length 14.5 mm. All appendages closely appressed; setae sparse, similar to last instar. *Head*: Vertex simple, rounded; epicranial suture indistinct. Antennae well defined, filiform, extending nearly to caudal margin of wings. Labrum well defined, square, with rounded corners; mandibles represented by triangular, rounded regions adjacent to, and caudo-laterad of labrum; labial palpus narrow, attenuate, ca 1.2 "x" as long as labrum; maxillae well developed, extending ca 0.33 from eyes to caudal margin of wings.

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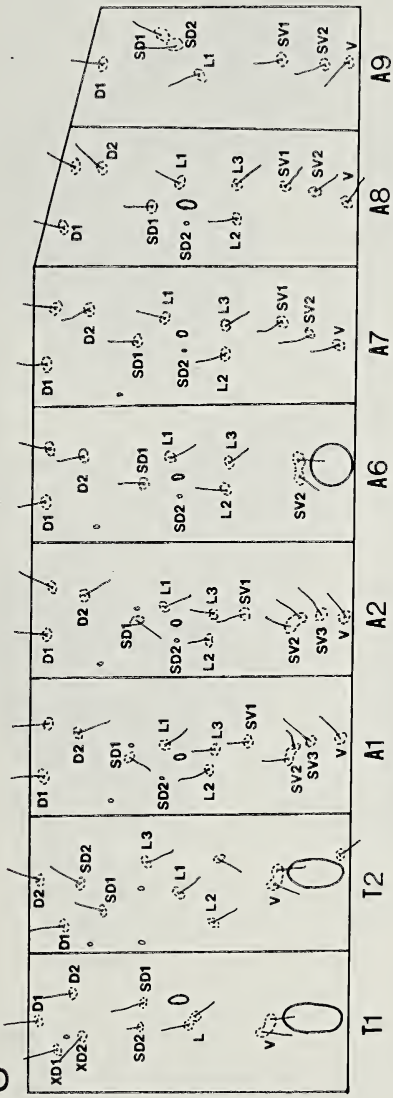

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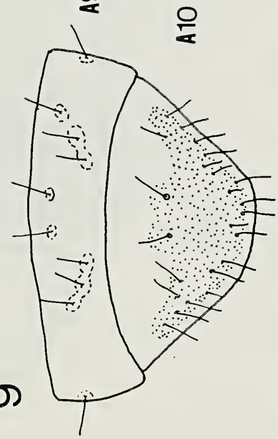

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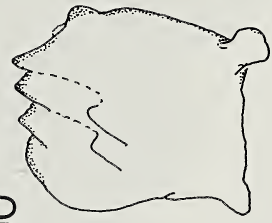

Fig. 8. Setal map of last instar, T1–2, A1–2, A6–9; lateral view, anterior at left.
Fig. 9. Setal map of A9–10; dorsal view.
Fig. 10. Left mandible, mesal view.

Thorax: Prothorax dorsally a narrow collar; ventrally with legs well defined, extending slightly less caudad than antennae. Mesothorax dorsally broad with moderate, mesal, longitudinal, sclerotized hump; ventrally with legs well defined, extending slightly caudad of anten-

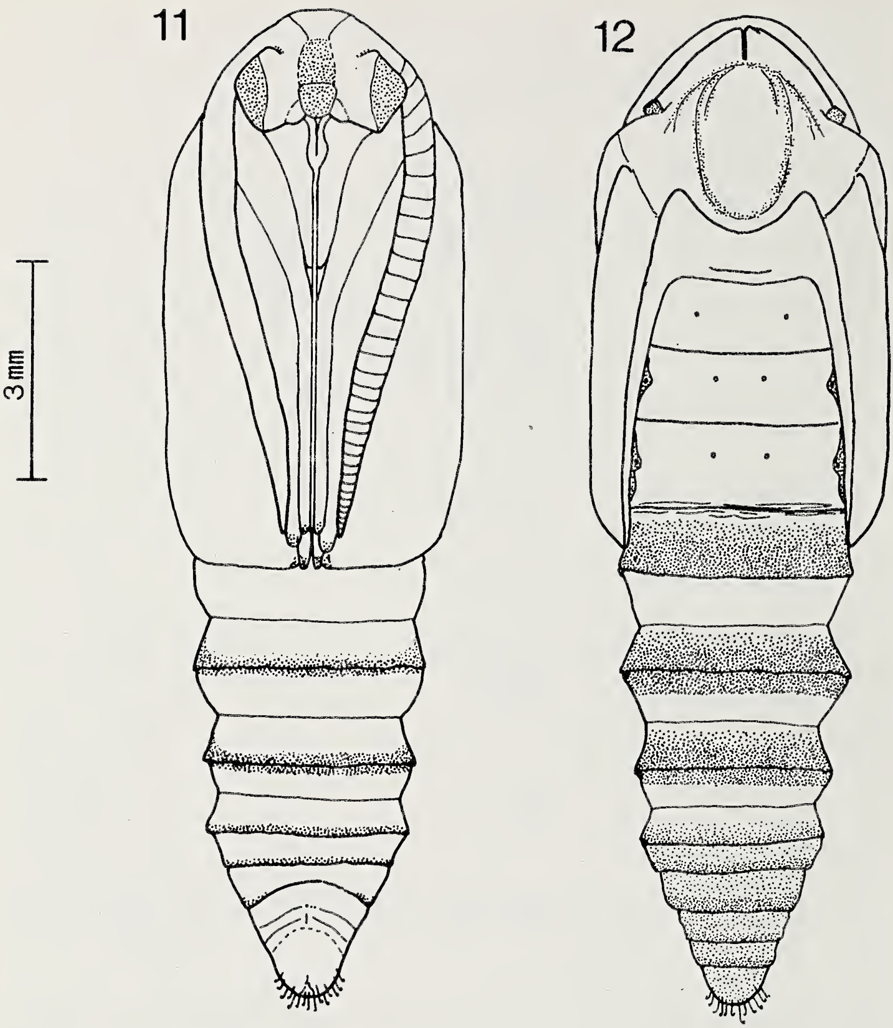

Fig. 11. Pupa of *Doa dora*; ventral view.
Fig. 12. Pupa of *Doa dora*; dorsal view.

nae. Metathorax dorsally a moderate transverse band, with strongly u-shaped margin anteriorly; margin of hindwings conspicuous along entire latero-dorsum. *Abdomen*: Spiracles 1–2 concealed beneath wings; spiracles 3–8 with strongly sclerotized peritreme. Cremaster indistinct with numerous long, distally-hooked bristles. The entire pupa is brown, translucent, and shiny.

The cocoon is an unusual, single layered, wiry, open mesh, nearly twice the volume of the pupa; the cast larval skin and head capsule are included within the cocoon.

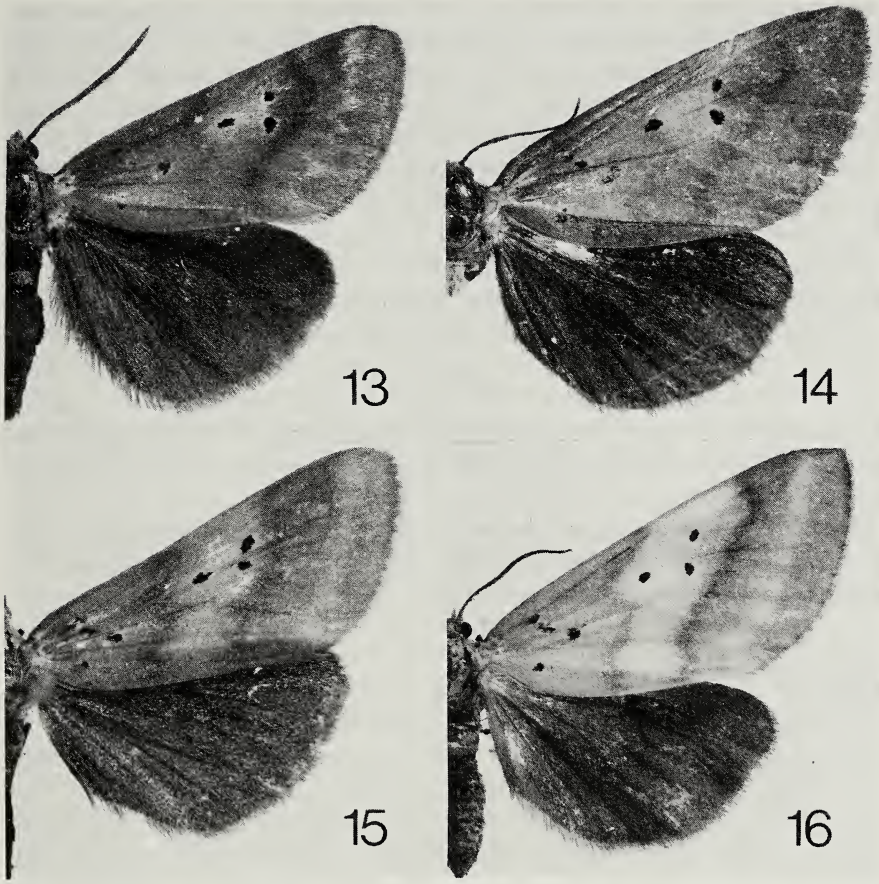

Fig. 13–16. Adults of *Doa dora*: **13)** Male from Baja California; **14)** Female from Baja California; **15)** Male from Colima; **16)** Female from Nayarit.

Biology and Ecology

Doa dora (TL: Guadalajara, Jalisco, Mexico) (Figs. 13–16) is widespread throughout northwestern Mexico, ranging from Baja California to Tamaulipas, and as far south as Colima and Cuernavaca (label data). Although adults have not been taken in the United States, larvae have been collected in San Diego, California (Oceanside, 27-XI-76, on Wandering Jew [Commelinaceae], D. K. Faulkner, SDNHM). Specimens from Baja California and Sonora may represent a closely related, undescribed species. The same is likely for specimens from Tamaulipas. Females from northwestern Mexico are distinguished from typical *D. dora* by a more uniform gray forewing; males possess a large, round, sclerotized region at the base of the valva lacking in *D. dora*. In addition to *D. dora*, the genus includes *D. ampla, D. raspa, D.*

cubana Schaus, *D. translucida* Dognin, and several undescribed species from Mexico and Costa Rica. The relationship of *Leuculodes* to *Doa* has not been examined in a phylogenetic context. The two appear to represent sister taxa, although it is posible that they represent a single genus. The group is in need of systematic revision.

In captivity, eggs of *Doa dora* are laid in irregular, contiguous, parallel rows on the leaves and stems of the host. On Isla de Cedros, the larval host is *Euphorbia misera*. Owing to the limited distribution of *E. misera* (Munz 1974; Wiggins 1980), other euphorbiaceous plants also must serve as larval hosts for *Doa dora*. Early instars live and feed within a loose communal nest, dispersing and feeding externally on the leaf surface in later stages. Early instar larvae will drop by a line of silk when disturbed. In the laboratory, pupation occurred in debris at the base of the host material. Developmental periods were as follows: 10–12 days as ovum; 30–35 days as larva; 15–18 days as pupa.

Females of *D. dora* appear to be partially diurnal, males appear to be more so. The flight is weak and fluttering, similar to *Ctenucha* species. Both sexes are attracted to blacklight (UV).

Discussion

The doids traditionally have been shuffled from family to family by various authors who have based their hypotheses on adult morphological characters. In the most recently proposed classification of the nearctic Lepidoptera, Franclemont (1983) erected the tribe Doaini in the Pericopinae (considered a subfamily of the Arctiidae), to accommodate the genera *Doa* and *Leuculodes*. However, characters of the larvae contradict this placement.

According to Habeck (1987), pericopid and arctiid larvae, respectively, are characterized by the presence of 3 and 4 verrucae above the coxae on T2 and T3, and heteroideous crochets (except for some lithosiines); the head is moderate in size, and integumental spicules are absent. In contrast, doid larvae lack verrucae on the thoracic coxae, have homoideous crochets, the head is very small, and the integument is covered with spicules.

Doid larvae share no uniquely derived characters with lymantriid larvae. Symplesiomorphies include typical noctuoid chaetotaxy and hypognathous head, elliptical spiracles, homoideous crochets, and fully developed abdominal prolegs. Doids lack the abundant secondary setae, which are responsible for the superficial similarity between lymantriids and arctiids, have biordinal as opposed to uniordinal crochets, and lack the fleshy, eversible middorsal gland on A7, which appears to represent an autapomorphy for the Lymantriidae.

Notodontids, likewise, share many noctuoid symplesiomorphies with the doids, but notodontid larvae can be distinguished from doids by

their modified A10 prolegs (sometimes reduced to peg-like structures), and the presence of two MD setae on T3 of the first instar (Hinton 1946), which appears to represent an autapomorphy for the Notodontidae.

The dioptids, which probably represent a specialized group within the Notodontidae, can be distinguished from doids by their larger head (larger than prothorax) and uniordinal crochets. Although the larva of *Phryganidia californica* Packard is similar in general facies to that of *Doa dora*, and possess integumental spicules that are remarkably similar to those of doids, features of the chaetotaxy, crochet arrangement, and mandibular configuration suggest that the two are not closely related.

The unique combination of larval characters possessed by doids appears to contradict traditional assignments of this group to lepidopterous families of similar adult morphology. It is likely that an increased knowledge of the distribution and significance of larval and pupal characters among the various clades of the Noctuoidea may lead to a greater understanding of phylogenetic relationships within this superfamily.

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The Lepidoptera of a central florida sand pine scrub community

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Abstract. A Lepidoptera survey was conducted between September 1982 and April 1985 in the Sand Pine Scrub area of Blue Spring State Park,· Volusia County, Florida. A total of 633 species comprising 43 families was recorded, including at least 12 undescribed species and one verified state record. Abundance and monthly distribution records are listed for moths. A floristic study of the scrub was also conducted.

Introduction

Blue Spring State Park is located in the west-central portion of Volusia County just outside of Orange City, Florida. (Fig. 1). The area consists of 590 hectares (1459 acres) of scrub, flatwoods, hammock, swamps, marshes, and riverine environments, and has a subtropical maritime climate. Volusia County has a mean temperature of about 21°C, and the mean annual rainfall is 1250mm. About 60% of the annual rainfall occurs between the first of June and the middle of October (USDA 1980). Volusia County sits within the lower Atlantic Coastal Plain. The surface is covered with sandy marine sediments from the late Pleistocene to Recent Age. Blue Spring is located on the extreme western edge of the Deland Ridge, an ancient sand dune formed during an interglacial period approximately 125,000 years ago.

With the cooperation of the Florida State Park Service, professional and amateur lepidopterists have begun to accumulate much-needed data on Florida Lepidoptera. Extensive surveys are being conducted in north and south Florida at Torreya and Collier-Seminole State Parks, respectively. The present study was done to provide additional distribution records for Lepidoptera, with a emphasis on moths, in the north-central region of Florida by concentrating on one specific, and little studied but important endemic plant community, the Sand Pine Scrub. Monthly distribution and abundance figures for all moth species were compiled, along with a floristics survey of the scrub.

Methods & Materials

Lepidoptera were collected an average of five times per week from September 1982 to April 1985. Collecting permits were issued annually from the Florida Department of Agriculture and Deparment of Natural Resources. Butterflies were recorded by collecting or by field sightings, but all moths were recorded

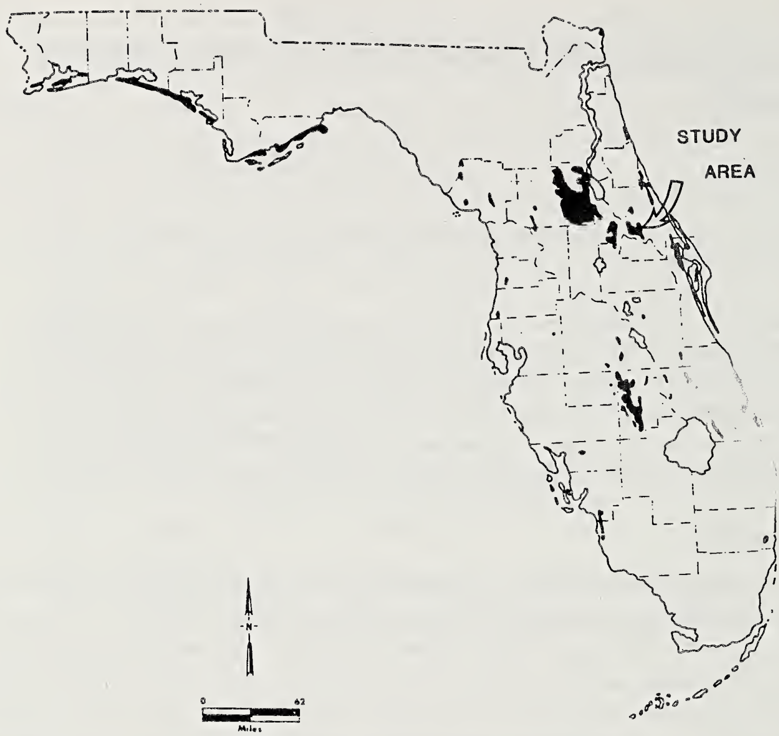

Fig. 1. Study site and distribution of sand pine scrub.

only by collecting. Moths were collected at all hours except 0300 to 0600. Ten existing mercury vapor lights on various park buildings were the primary source for moths. Occasionally, filtered black lights were also used. A portable generator was used in areas inaccesible to electricity. A bait of molasses, sugar, and stale beer was brushed on tree bark, primarily to catch members of the genera *Catacola* and *Zale*. The pheromone 3, 13–octadecadien-1-OL acetate (ZZ-ODDA) was used to collect 3 of the 4 species of Sesiidae. Macrolepidoptera were collected in cyanide and ethyl acetate killing jars. Microlepidoptera were collected in small vials and frozen to prevent damage. Several species appeared for only one or two months but were found in higher numbers than other species recorded for five or six months. Therefore, monthly distribution was not considered in determining abundance of each species. Abundance was determined by the total number of specimens observed during the 32 month collecting period. The following criteria were used: uncommon (1-5 specimens), occasional (6-20), common (21-50), abundant (51+). New species are indicated in the checklist as n. sp. A question mark preceding a generic or specific name indicates an uncertain determination.

Approximately one-third of the Lepidoptera were identified through the taxonomic literature. Those references included Blanchard (1979), Blanchard & Knudson (1983), Cashatt (1984), Covell (1984), Eichlin & Cunningham (1978), Hodges et al. (1983), Hodges (1986), Holland (1968), Howe (1975), Kimball (1965), Klots (1951), Maxwell (1981), Mitchell & Zim (1977), Rockburne &

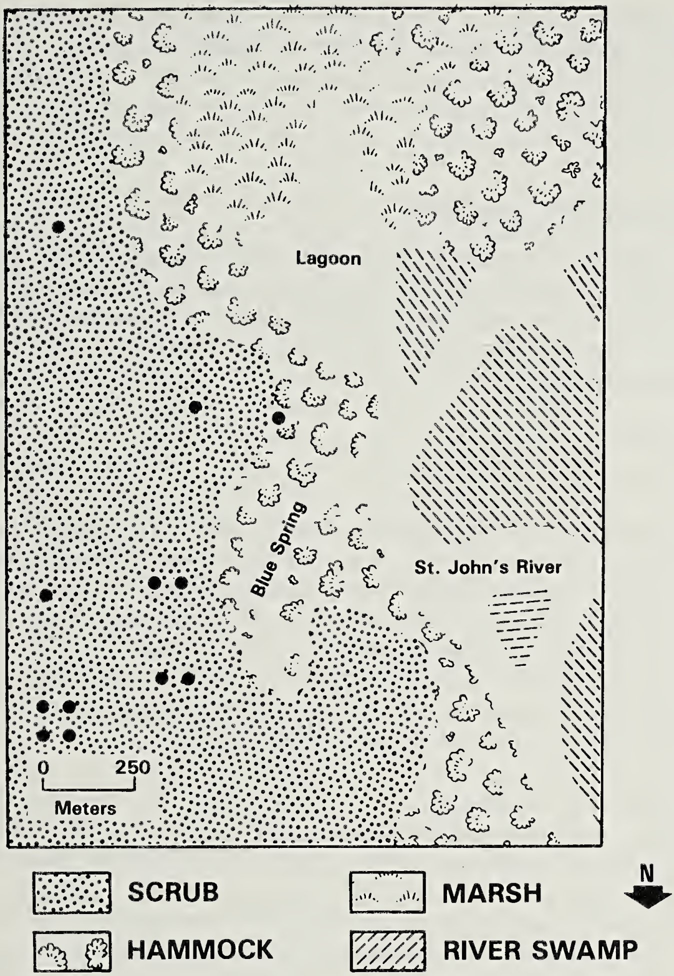

Fig. 2. The vegetation of Blue Spring State Park. Collecting sites are indicated by circles.

Lafontaine (1976), and the USDA (1975). Approximately one-third were identified through the use of a comparative collection at the Florida Department of Agriculture, Division of Plant Industry, Gainesville, Florida. The final third were identified by D. Baggett, L. Dow, & J. Heppner. Forty species of microlepidoptera were deposited in the Division of Plant Industry collection (FSCA), while all others remained in the private collection of the author.

A survey of the plants found in the scrub of Blue Spring was conducted between April and August 1986. Plants were prepared with a standard leaf press, then identified, mounted, and labeled. Voucher specimens of all vascular plants collected are on deposit in the Florida State Museum's Herbarium (FLAS), University of Florida, Gainesville. References used for plant identification included Cronquist (1980), Duncan (1967), Duncan & Foote (1975), Grimm

(1966), Kartesz (1980), Kurz & Godfrey (1962), Radford et al. (1968), Tarver et al. (1979), USDA (1982), and Wunderlin (1982).

Description of Study Area

Some moths not normally associated with a scrub environment were collected. Since Lepidoptera may fly from one area to another, plant species in several other plant communities surrounding the scrub may be serving as larval food hosts. Therefore, the common vegetation of these communities was also included in this study (FIG. 2).

HAMMOCK

Bordering the scrub throughout the park is a mesic mixed hardwood hammock. The dominant species include *Sabal palmetto* (Walt.) Lodd. ex Schult., *Quercus virginiana* Mill., *Q. laurifolia* Michx., *Liquidamber styraciflua* L., and *Magnolia grandiflora* L. Common understory species include *Quercus nigra* L., *Carya glabra* (Mill.) Sweet, *Arilia spinosa* L., *Asimina parviflora* (Michx.) Dunal, *Callicarpa americana* L., and *Gelsemium sempervirens* (L.) St. J. H. Hil. Other common plants include *Phlebodium aureum* (L.) Small, *Polypodium polypoidioides* (L.) Watt, *Vittaria lineata* (L.) J. Smith, *Mitchella repens* L., *Epidendrum conopseum* R. Br., *Ruellia caroliniensis* (J.F.Gmel.) Steud., *Salvia lyrata* L., and *Elaphantopus elatus* Bertol.

FLATWOODS & BAYHEAD

A major part of the flatwoods is dominated by *Pinus elliottii* Engelm. with a thick understory of *Serenoa repens* (Bartr.) Small. Other important shrubs include *Ilex glabra* (L.) A. Gray, *Lyonia fruticosa* (Michx.) G.S. Torr., *L. lucida* (Lam.) K. Koch and *Asimina reticulata* Shuttlew. ex Chapm. Herbaceous plants include *Liatris tenuifolia* Nutt., *Sabatia brevifolia* Raf., *Polygala nana* (Michx.) DC, *P. lutea* L., *Eriocaulon compressum* Lam., and *Lachnocaulon anceps* (Walt.) Morong. In the more poorly drained sites the dominant pine is typically *Pinus serotina* Michx. Herbaceous plants in this area include *Pinguicula pumila* Michx., *Drosera* sp., *Utricularia* sp., and *Hypoxis* sp. These soils become even further saturated as a flatwoods depression forms a small bayhead on the south edges of the park. The characteristic trees of this area are *Taxodium distichum* (L.) L. Rich., *Persea palustris* (Raf.) Sarg., *Gordonia lasianthus* (L.) Ellis, and *Magnolia virginiana* L. Understory plants include *Smilax glauca* Walt., *Woodwardia areolata* (L.) Moore, *Osmunda cinnomomea* L., and *O, regalis* L.

FLOODPLAIN FORESTS

Also known as river swamps, these areas border the St. Johns River and are constantly inundated. These deciduous hardwood swamps consist of *Sabal palmetto, Taxodium distichum, Carya aguatica* (Michx.) Nutt. ex Ell., *Nyssa biflora* (Walt.) D. Sarg., *Acer rubrum* L., *Fraxinus caroliniana* Mill., and *Cornus foemina* Mill. Common herbaceous plants include *Saururus cernuus* L., *Thalia geniculata* L., *Crinum americanum* L., and *Aster caroliniana* Walt.

AQUATIC ENVIRONMENTS

These areas include the spring run, lagoon, freshwater marsh, and streambanks. The marshes are dominated either by *Spartina bakeri* Merr. or *Panicum hemitomon* Schult. Commonly scattered along marsh edges are woody species such as *Salix caroliniana* Michx., *Sambucus canadensis* L., and *Cephalanthus occidentalis* L.

The open areas of the river, lagoon, and spring run include plants such as *Pistia stratiotes* L., *Eichhornia crassipes* (Mart.) Solms, *Nuphar luteum* (L.) Sibth. + J.E. Smith, *Ceratophyllum demersum* L., and *Salvinia minima* Baker.

Many plants found along the banks of these waters occur naturally or were washed in from the river. Common species along the waters edge include *Sagittaria latifolia* Willd., *Alternantha philoxeroides* (Mart.) Griseb., *Pontederia cordata* L., *Kosteletzkya virginica* (L.) Presl ex A. Gray. *Hibiscus coccineus* (Medic.) Walt., *Amaranthus australis* (A. Gray) Sauer, *Vigna luteola* (Jacq.) Benth., *Lythrum salicaria* L., and *Paspalum repens* Berg.

SCRUB

Several times during Florida's history, the sea levels were higher than they are today and the coastline was much further inland. Sand dunes formed along these ancient shorelines and still persist today. These are the natural sites of the Sand Pine Scrub community in Florida (DNR 1975). With the exception of a few locations in Alabama, the Sand Pine Scrub is restricted to the state of Florida (Laessle 1958). The scrub consists of well-drained, fine white siliceous sands and is composed almost entirely of thick growths of broad-leaved evergreen shrubs. Because of the sterile soils, there is very little diversity among the herbaceous plants. Although a fire-dependent community, ground cover is sparse and leaf litter accumulates very slowly. Therefore, fires are infrequent, perhaps every 20 to 40 years. When a fire does occur, it will burn hot enough to allow the serotinous cones of the Sand Pine to open and begin dropping seeds. If a scrub is not exposed to fire, it will most likely succeed into a xeric hammock (Monk 1968). Due to their dry upland locations, scrub environments are rapidly being lost to real estate development, and therefore are considered highly endangered areas (DNR 1975).

The Sand Pine Scrub of Blue Spring is part of a much larger scrub which extends south and east through Orange City and Deltona. Due to the growth of the area, especially in Deltona, this scrub is disappearing. The scrub within the boundaries of Blue Spring consists of approximately 202 hectares (500 acres), situated on soils of Daytona and Paola fine sand (USDA 1980). North and east of the park, nearly 200 more hectares continue to occur on Apopka fine sands until they meet a Longleaf Pine/Turkey Oak Sandhill area.

The overstory of the Blue Spring scrub is dominated by sand pine, (*Pinus clausa* (Chapm. ex Engelm.) Vasey ex Sarg.). The understory consists of three dominant scrub oaks: sand-live oak (*Quercus geminanta* Small), myrtle oak (*Q. myrtifolia* Willd.), and chapman oak (*Q. chapmanii* Sarg.). Other important shrubs include devilwood or wild olive (*Osmanthus americana* (L.) Benth. & Hook. f. ex Gray), scrub holly (*Ilex opaca* Ait. var. *arenicola* (Ashe) Ashe), carolina holly (*I. ambigua* (Michx.) Torr.), saw palmetto (*Serenoa repens*), silkbay (*Persea humilis* Nash), and rusty lyonia (*Lyonia ferruginea* (Walt.) Nutt.). The ground cover includes small leaved blueberry (*Vaccinium myrsi-*

nites Lam.), gopherapple (*Licania michauxii* Prance), and scattered lichens *Cladina* spp. Occasionally a scrub will lack sand pine all together, yet the understory will have the same species composition. This situation is found in a 20 hectare section of the park scrub.

Many of the sand pines in the park are beginning to degenerate. By 50 years of age, heartrot is a common occurrence. With such a dense understory, competition has made it difficult for sand pine to regenerate. Only in the highly disturbed areas such as old fire roads and borrow pits are the sand pine seedlings growing successfully. Due to the disturbed nature of this scrub, many successional plant species have invaded the area and this is resulting in a faster accumulation of leaf litter. Because of the campground and cabins, the high recreational use of the area makes it unfeasible for prescribed burning. With each passing year, the scrub accumulates large amounts of herbaceous and woody litter, both on the soil surface and in the trees. This suggests that the probability of a wildfire is greatly increased (Veno 1976).

Annotated List of Scrub Plants

The following is a list of plants recorded from the scrub of Blue Spring. Vascular plant nomenclature follows that of Wunderlin (1982). Genera and species within the families are arranged alphabetically.

PINACEAE
- *Pinus clausa* (Chapm. ex Engelm.) Vasey ex Sarg.

POACEAE
- *Andropogon glomeratus* (Walt.) BSP.
- var. *glaucopsis* (Ell.) Mohr.
- *Eustachys neglecta* (Nash) Nash
- *Panicum ciliatum* Ell.
- *P. commutatum* Schult.
- *P. miliaceum* L.
- *Paspalum notatum* Fluegge.
- *Setaria geniculata* (Lam.) Beauv.

CYPERACEAE
- *Rhynchospora megalocarpa* A. Gray

ARECACEAE
- *Serenoa repens* (Bartr.) Small

XYRIDACEAE
- *Xyris caroliniana* Walt.

JUNCACEAE
- *Juncus scirpoides* Lam.

SMILACEAE
- *Smilax auriculata* Walt.
- *S. glauca* Walt.
- *S. pumila* Walt.

AGAVACEAE
- *Yucca flaccida* Haw.

MYRICACEAE
- *Myrica cerifera* L.

FAGACEAE
- *Quercus chapmanii* Sarg.
- *Q. geminata* Small
- *Q. laurifolia* Michx.
- *Q. myrtifolia* Willd.

ULMACEAE
- *Ulmus americana* L.

POLYGONACEAE
- *Polygonella gracilis* (Nutt.) Meisn.

AMARANTHACEAE
- *Froelichia floridana* (Nutt.) Moq.

MAGNOLIACEAE
- *Magnolia grandiflora* L.

ANNONACEAE
- *Asimina obovata* (Willd.) Nash

LAURACEAE
- *Cinnamomum camphora* (L.) Presl
- *Persea humilis* Nash

BRASSICACEAE
- *Lepidium virginicum* L.

ROSACEAE
- *Prunus serotina* Ehrh.

CHRYSOBALANACEAE
- *Licania michauxii* Prance

FABACEAE

Amorpha fruticosa L.
Desmodium incanum DC.
D. tortuosum (Sw.) DC.
Galactia elliottii Nutt.
G. floridana Torr. & Gray
G. ? regularis (L.) BSP
Medicago lupulina L.
EUPHORBIACEAE
Chamaesyce hyssopifolia (L.) Small
Cnidoscolus stimulosus (Michx.) Engelm. & Gray
Croton glandulosus L.
EMPETRACEAE
Ceratiola ericoides Michx.
ANACARDIACEAE
Rhus copallina L.
AQUIFOLIACEAE
Ilex ambigua (Michx.) Torr.
I. opaca Ait. var. *arenicola* (Ashe) Ashe
VITACEAE
Ampelopsis arborea (L.) Koehne
Parthenocissus quinquefolia (L.) Planch.
Vitis aestivalis Michx.
V. rotundifolia Michx. (*munsoniana* Simpson of some authors)
CLUSIACEAE
Hypericum hypericoides (L.) Crantz.
H. reductum P.Adams
CISTACEAE
Helianthemum corymbosum Michx.
Lechea mucronata Raf.
PASSIFLORACEAE
Passiflora incarnata L.
CACTACEAE
Opuntia humifusa (Raf.) Raf.
ONAGRACEAE
Gaura angustifolia Michx.
Oenothera laciniata Hill
APIACEAE
Apium leptophyllum (Pers.) Muell.
ERICACEAE
Befaria racemosa Vent.
Gaylussacia dumosa (Andrz.) T. & G.
G. tomentosa (A. Gray) Small
Lyonia ferruginea (Walt.) Nutt.
L. lucida (Lam.) K. Koch
Vaccinium myrsinites Lam.
V. stamineum L.
SAPOTACEAE
Bumelia tenax (L.) Willd.
EBENACEAE
Diospyros virginiana L.
OLEACEAE
Osmanthus americana (L.) Benth. & Hook. f. ex Gray
LOGANIACEAE
Polypremum procumbens L.
ASCLEPIADACEAE
Asclepias tomentosa Ell.
CONVOLVULACEAE
Ipomoea pandurata (L.) G.F.W. Mey
Merremia dissecta (Jacq.) Hall. f.
POLEMONIACEAE
Phlox drummundii Hook.
VERBENACEAE
Callicarpa americana L.
LAMIACEAE
Hyptis mutabilis (A. Rich) Briq.
Monarda punctata L.
Salvia lyrata L.
Teucrium canadense L.
Trichostema dichotomum L.
SCROPHULARIACEAE
Gratiola hispida (Benth.) Pollard
Linaria canadensis (L.) Dum.
Seymeria pectinata Pursh.
BIGNONIACEAE
Campsis radicans (L.) Seem. ex Bureau
RUBIACEAE
Diodia teres Walt.
Richardia brasiliensis (Moq.) Gomez
ASTERACEAE
Baccharis halimifolia L.
Berlandiera subacaulis (Nutt.) Nutt.
Bidens alba (L.) DC.
Carphephorus corymobsus (Nutt.) Torr. & Gray
C. odoratissimus (J.F.Gmel.) Herb.
Erigeron strigosus Muhl.
Eupatorium compositifolium Walt.
Garberia heterophylla (Bartr.) Merr. & Harp.

Gnaphalium falcatum Lam.
Heterotheca subaxillaris (Lam.) Britt. & Rusby
Hieracium megacephalon Nash.
Krigia virginca (L.) Willd.
Lactuca graminifolia Michx.
Pityopsis graminifolia (Michx.) Nutt.
Pterocaulon virgatum (L.) DC.
Pyrrhopappus carolinianus (Walt.) DC.
Solidago sp.
Vernonia gigantea (Walt.) Trel. ex Branner & Coville

Results & discussion

A total of 633 species of Lepidoptera were recorded, consisting of 591 moths and 42 butterflies in 43 families. Families with the most species recorded were Noctuidae (172), Pyralidae (100), and Tortricidae (76). The average monthly distribution curve shows that the greatest species diversity occurred in the spring, and the least diversity in the summer (Fig. 3). The highest total was in March (201 species) and the lowest was in July (32 species). The fall, winter, and spring months were surveyed for three years, while the summer months were surveyed for only two years. Thus, sampling time may account in part for the lower number of species throughout June, July, and August.

#226, previously known from Florida as *E. poaphilodes*, is now listed as *E. fergusoni* (Solis 1986). #197 is unconfirmed as being collected within the boundries of Blue Spring. #555 is unconfirmed as the specimen is missing. #506 was identified from the casings. #485 was collected at light and not with the Sesiidae pheromone. Heppner (personal communication) indicated that the collection of #134 *Phyllonorycter fitchella* (Gracillariidae) represented the first report of this species in Florida. Twelve other microlepidoptera were determined by Heppner as being new species, most or all of which should be state records upon their description. Doug Ferguson, of the Smithsonian Natural History Museum, and David Baggett (personal communication), indicated that #129 is probably a worn specimen of *frondaria* or *N. bifiliata*, and its very faded condition makes a final determination unlikely. *Synchlora aerata* has yet to be recorded this far south. Baggett indicates that #187 identified here as *Arugisa latiorella*, may be *A. watsoni* Richards. Baggett also mentioned that #257, #258, and #559 may be state records and, upon future examination by taxonomists, the list should contain other state records as well as hundreds of county records. This study has facilitated a better understanding of the distribution of Florida Lepidoptera, and should also provide the basis for further investigations into host plant relationships and possible endemic lepidopterans of scrub environments.

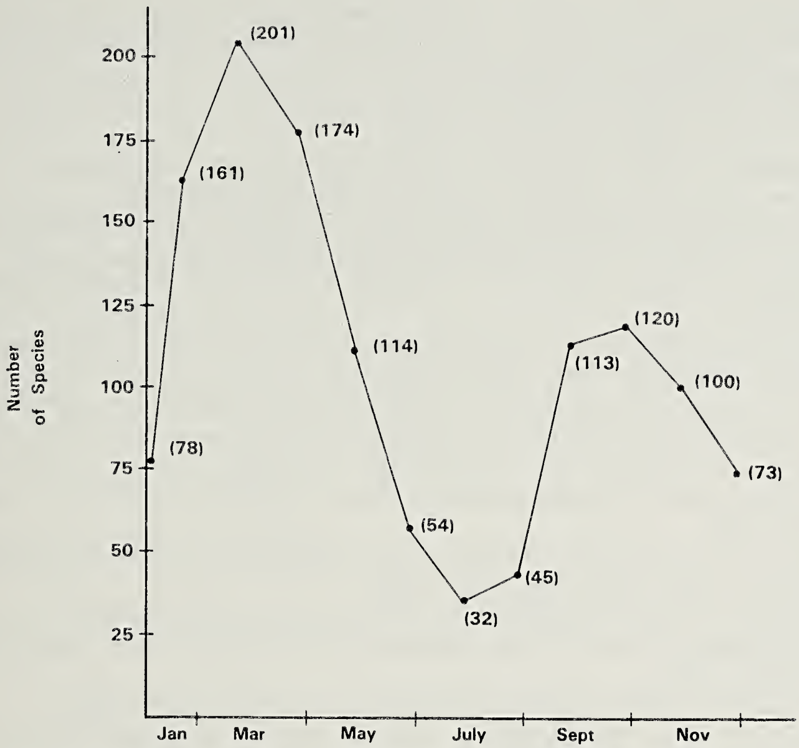

Fig. 3. Average monthly distribution of moth species between September 1982 and April 1985.

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Table 1. Complete listing of Lepidoptera of Blue Spring — Abundance indicated by C = common, O = occasional, U = uncommon, A = abundance

	Abundance	Month
APATELODIDAE		
1 Olceclostera indistincta (Hy. Edw.)	C	- F M - - - - - - - - -
ARCTIIDAE		
2 Afrida ydatodes Dyar.	A	J F M - - - - - S O N -
3 Cisseps fulvicollis (Hbn.)	U	- - - - - - - - - - N -
4 Cisthene packardi (Grt.)	C	- F M - - - - - - - N -
5 Cisthene striata Ottol.	A	- - M A M - - - - - N -
6 Cisthene subjecta Wlk.	A	J - M A M - - - - O N -
7 Cisthene tenuifascia Harv.	O	- - - A - - - - - - - -
8 Clemensia albata Pack.	A	J - M A - - - - - - - -
9 Cosmosoma myrodora Dyar	O	- F - - - - - - - - N D
10 Crambidia lithosioides Dyar	O	- - - - - - - - - - N -
11 Ecpantheria scribonia (Stoll)	O	- - M - - - - - - - - -
12 Estigmene acrea (Drury)	U	- - M - - - - - - - - -
13 Euerythra phasma Harv.	O	- F M - - J - - - - - -
14 Grammia nais (Drury)	C	J F - - - - - A S - - -
15 Halysidota tessellaris (J.E.Smith)	C	- F - - M J - - S - - -
16 Holomelina aurantiaca (Hbn.)	C	J F M A - - - - - - - -
17 Holomelina ferruginosa (Wlk.)	C	- F M - - - - - - - - -
18 Holomelina laeta (Guer.-Meneville)	U	- - - - - - - - - - - D
19 Holomelina opella (Grt.)	U	- F M - - - - - - - - -
20 Holomelina rubicundaria (Hbn.)	U	- - - A - - - - - - - -
21 Hyphantria cunea (Drury)	A	J F M - - - - - S - - -
22 Hypoprepia miniata (Kby.)	A	- - - A M - - - - O - -
23 Leucanopsis longa (Grt.)	U	- - - - - - - - - - - D
24 Pyrrharctia isabella (J.E.Smith)	O	- F - - - - - - - - - -
25 Spilosoma congrua Wlk.	U	J F - - - - - - - - - -
26 Utetheisa bella (L.)	C	J - - - - - - - - - N -
BLASTOBASIDAE		
27 Glyphidocera lactiflosella (Cham.)	C	- - - - - - - - S O - -
28 Holcocera ? lepidophaga Clarke	C	- - M A - - - - - - - -
29 Valentinia glandulella (Riley)	C	- - - - - - - - - O - -
30 sp.	U	- - M A - - - - - - - -
COCHYLIDAE		
31 Aethes sp.	U	- - M - - - - - - - - -
32 Aethes sp.	U	- - - - - - - - - - - D
33 Aethes sp.	U	- - - - - - - - - - - D
34 Aethes sp.	U	- - - - - - - - - - - D
35 Aethes sp.	O	- - M A - - - - S O N -
36 Carolella bimaculana (Rob.)	C	- - - A M J J - - O N -
37 Carolella erigeronana (Riley)	O	- - - A - - J - - - - -

Table 1 (Continued)

	Abundance	Month
38 Carolella sartana (Hb.)	O	- - - A - - - - - - - -
39 Hysterosia argentilimitana Rob.	O	J F - A - - - - - - - -
COLEOPHORIDAE		
40 Homaledra sabalella (Cham.)	U	- - - A - - - - - - - -
COSMOPTERIGIDAE		
41 Cosmopterix prob. gemmiferella Clem.	U	- F M - - - - - - - - -
42 Euclemensia bassettella (Clem.)	U	- - - - - - - A S - - -
43 Perimede erransella Cham.	U	- - M - - - - - - - - -
COSSIDAE		
44 Givira francesca (Dyar)	U	- - - A - - - - - - - -
45 Prionoxystus robiniae (Peck)	U	- - M - - - - - - - - -
DREPANIDAE		
46 Eudeilinea luteifera Dyar	U	- - - - - - - - S - - -
ERIOCRANIDAE		
47 Eriocraniella mediabulla Davis	U	- - - A - - - - - - - -
GELECHIIDAE		
48 Anacampsis coverdalella Kft.	O	- - - - M - - - - - - -
49 Aristotelia roseosuffusella (Clem.)	O	J - M - M - - - - - - -
50 Aristotelia sp.	U	- F - - - - - - - - N D
51 Aroga coloradensis (Bsk.)	A	J - - - - - - - - - N -
52 Dichomeris ? georgiella (Wlk.)	U	- F - - - - - - - - - -
53 Evippe prunifoliella Cham.	O	- F M - - - - - - - - -
54 Exoteleia pinifoliella (Cham.)	O	- F M - - - - - - - - -
55 Polyhymno luteostrigella Cham.	O	- - M - - - - - - - - -
56 ?Sinoe sp.	O	J F - - - - - - - - - -
57 Stegasta bosqueella (Cham.)	C	- - - A M - - - S O - -
58 Telphusa sp.	U	J - M - - - - - - - - -
59 Dichomeris ? xanthoa Hodges	U	- - - - - - - - - O - -
60 sp.	U	- - - A - - - - - - - -
61 sp.	U	- F - - - - - - - - - -
62 Dichomeris ? aglaia Hodges	U	- - - - - - - - - - - D
63 sp.	U	- - - A - - - - - - - -
64 sp.	U	- F - - - - - - - - - -
GEOMETRIDAE		
65 Anacamptodes defectaria (Gn.)	U	J F - - M - - - - - - -
66 Anacamptodes vellivolata (Hulst)	U	- - - A - - - - - - - D
67 Anavitrinella pampinaria (Gn.)	C	- F M - M - - - - - N -
68 Besma quercivoraria (Gn.)	U	- F M - - - - - - - - -
69 Caripeta aretaria (Wlk.)	O	J F M - - - - - - - - -
70 Chlorochlamys chloroleucaria (Gn.)	C	- F M A M - - - - - - -
71 Chloropteryx tepperaria (Hulst)	C	- F M A - - - - S O - -

Table 1 (Continued)

	Species	Abundance	Month
72	Cyclophora myrtaria (Gn.)	U	- - - - - - - - - O - -
73	Cymatophora approximaria Hbn.	C	- - - - - - - - - - N -
74	Dichorda iridaria latipennis (Hulst)	O	J F - - M - - - - O - -
75	Disclisioprocta stellata (Gn.)	U	- - - - - - - - S - - -
76	Dyspteris abortivaria H.-S.	O	- F M - - - - - - - - -
77	Epimecis hortaria (F.)	C	- F M - - - - - - - - -
78	Episemasia solitaria (Wlk.)	U	- - M A - - - - - - - -
79	Euchlaena amoenaria astylusaria (Wlk.)	O	- F - - - - - - S - - -
80	Euchlaena deplanaria (Wlk.)	O	- F M - - - - - S O N -
81	Eulithis diversilineata (Hbn.)	C	- - - - M - - - - O N -
82	Eupithecia miserulata Grt.	O	J - M - - - - - - - N D
83	Eusarca confusaria Hbn.	O	- F M - - - - - - - - -
84	Eusarca fundaria (Gn.)	U	- - - - - - - - - O - -
85	Eutrapela clemataria (J.E.Smith)	A	- F M - - - - - - - - -
86	Glenoides texanaria (Hulst)	A	J F M - - - - - - - - D
87	Hethemia pistasciaria insecutata (Wlk.)	U	- - M - - - - - - - - -
88	Hydriomena pluviata meridianata McD.	O	- - M A - - - - - - - -
89	Hypagyrtis esther (Barnes)	C	J F - A M - J - - O N -
90	Hypomecis umbrosaria (Hbn.)	U	- - M - - - - - - - - -
91	Idaea demissaria (Hbn.)	C	- - - A M - - - S O - -
92	Idaea eremiata (Hulst)	U	- - - A - - - - - - - -
93	Idaea ostentaria (Wlk.)	U	- - - - - - - - - O - -
94	Idaea tacturata (Wlk.)	O	- - - A - - - - S O N -
95	Lambdina pultaria (Gn.)	U	- - - A - - - - - - - -
96	Leptostales pannaria (Gn.)	O	J F - - - - - - - - N D
97	Lobocleta peralbata (Pack.)	U	- - M - - - - - - - - -
98	Lophosis labeculata (Hulst)	A	J F M A - - - - S - N -
99	Lychnosea intermicata (Wlk.)	U	- - - A - - - - - - - -
100	Lycia ypsilon carlotta (Hulst)	C	- F M - - - - - - - - -
101	Melanolophia canadaria (Gn.)	O	- - M A - - - - - - - -
102	Metarranthis homuraria (G.& R.)	U	- F M - - - - - - - - -
103	Metarranthis obfirmaria (Hbn.)	U	- - M - - - - - - - - -
104	Nacophora quernaria (J.E.Smith)	C	- F M - - - - - - - - -
105	Nematocampa limbata (Haw.)	O	- - - A M - - - - - - -
106	Nemoria b. bifiliata (Wlk.)	C	- F M A M - J A - O - -
107	Nemoria catachloa (Hulst)	C	- F M A M - J - S - N -
108	Nemoria elfa Fgn.	C	- F - - - - - - - O N D
109	Nemoria lixaria (Gn.)	A	J - M A M J J - S O - D
110	Nemoria saturiba Fgn.	U	- - - A M - - - - - - -
111	Nepheloleuca floridata (Grt.)	U	- - - - - - - A - - - -
112	Orthonama centrostrigaria (H.-S.)	C	J F - A - - - - - - - D
113	Orthonama obstipata (F.)	U	- F - - - - - - - - - -
114	Patalene olyzonaria (Wlk.)	C	- - M - - - - - S - N -

Table 1 (Continued)

	Abundance	Month
115 Phigalia strigataria (Minot)	U	- - M - - - - - - - - -
116 Phrudocentra centrifrugaria (H.-S.)	U	- - - - - - - - - O - -
117 Pleuroprucha insulsaria (Gn.)	U	- - - - - - - - - O N D
118 Prochoerodes transversata incurvata (Gn.)	O	- - - - M - - - - - - -
119 Protoboarmia porcelaria (Gn.)	O	- F M - - - - - - - - -
120 Scopula aemulata (Hulst)	U	- F - - - - - - - - - -
121 Scopula compensata (Wlk.)	U	J - - - - - - - - - N -
122 Scopula lautaria (Hbn.)	O	J F M A - - - - - - - D
123 Scopula timandrata (Wlk.)	U	- - M - M - - - - - - -
124 Semiothisa bicolorata (F.)	C	J - M - M - - - - - N D
125 Semiothisa distribuaria (Hbn.)	U	- - - - M - - - - - - -
126 Semiothisa gnophosaria (Gn.)	U	J - - A - - - - - - - -
127 Semiothisa sanfordi Rindge	C	J F M A M - - - S O N -
128 Stenaspilatodes antidiscaria (Wlk.)	U	- F - - - - - - - - - -
129 Synchlora looks like aerata (F.)	U	- - - - - - - - - O - -
130 Synchlora frondaria Gn.	C	J F M A - J - - S - N -
131 Synchlora gerularia (Hbn.)	C	- F M A - - J - - - N D
132 Tornos scolopacinarius spodius Rindge	C	- F M A - - - - - - - -
GLYPHIPTERIGIDAE		
133 Diploschizia sp.	U	- - - A - - - - - - - -
GRACILLARIIDAE		
134 Phyllonorycter fitchella (Clem.)	U	- - - - - - - - - O - -
135 sp.	U	- - M - - - - - - - - -
136 sp.	U	- - - - - - - - - O - -
137 sp.	U	- - - A - - - - - - - -
INCURVARIIDAE		
138 Adela caeruleella Wlk.	U	- - M - - - - - - - - -
LASIOCAMPIDAE		
139 Artace cribraria (Ljungh)	C	- - M - - - - - - O N -
140 Malacosma americana (F.)	A	- - M A - - - - - - - -
141 Malacosma disstria Hbn.	A	- - - - M - - - - - - -
142 Phyllodesma americana (Harr.)	C	- F M A - - - - - - - -
143 Tolype minta Dyar	U	- - - - - - - - S - - -
144 Tolype notialis Franc.	C	J - M A - J - - S - N D
LIMACODIDAE		
145 Adoneta spinuloides (H.-S.)	U	- - - - - - - - S - - -
146 Apoda Y-inversa (Pack.)	U	- - M - - - - - - - - -
147 Apoda rectilinea (G.& R.)	C	- - - A - J - - S - - -
148 Euclea delphinii (Bdv.)	A	- - M A M J - - - - N D
149 Isa textula (H.-S.)	A	- - - - - - - - S O N D
150 Isochaetes beutenmulleri (Hy.Edw.)	U	- - - - - - - A - - - -
151 Lithacodes gracea Dyar	O	- - - A - - J - - - - -
152 Monoleuca erectifascia Dyar	U	- - - - - J - - - - - -

Table 1 (Continued)

	Abundance	Month
153 Monoleuca near semifascia (Wlk.)	U	- - - - - - J - - - - -
154 Monoleuca subdentosa Dyar	A	- - - A - J J - S - - -
155 Natada nasoni (Grt.)	U	- - - - - J - - - - - -
156 Prolimacodes badia (Hbn.)	A	- - - A - J J - S - - -
157 Sibine stimulea (Clem.)	C	- - - - - - J - S O N -
LYMANTRIIDAE		
158 Dasychira leucophaea (J.E.Smith)	O	- - - A - - - - - - - -
159 Dasychira manto (Stkr.)	C	J - M - M - - - - - N -
160 Dasychira tephra Hbn.	O	- - - - M - - - - O - -
MEGALOPYGIDAE		
161 Lagoa lacyi B.& McD.	C	- - - - M J J - - - - -
162 Megalopyge opercularis (J.E.Smith)	A	- - - - M J J - S - - -
MIMALLONIDAE		
163 Cicinnus melsheimeri (Harr.)	U	- - - - M - - - - - - -
MOMPHIDAE		
164 Mompha eloisella (Clem.)	O	- - - A - - - - - - - -
NEPTICULIDAE		
165 ?Ectodemia sp.	U	- - - - - - - - - - - D
NOCTUIDAE		
166 Abablemma brimleyana (Dyar)	O	- - M A - - - - - O N -
167 Acronicta afflicta Grt.	U	- - - - - - - - S - - -
168 Acronicta americana (Harr.)	U	- - M - - - - - - - - -
169 Acronicta brumosa Gn.	U	- - M A - - - - - - - -
170 Acronicta hasta Gn.	U	- F - - - - - - - - - -
171 Acronicta impleta Wlk.	U	- F M - - - - - - - - -
172 Acronicta lanceolaria (Grt.)	U	- - M - - - - - - - - -
173 Acronicta oblinita (J.E.Smith)	U	J - - - - - - - - - - -
174 Acronicta tritona (Hbn.)	O	- - M - - - - - - - N -
175 Acronicta vinnula (Grt.)	O	J F - - - - - A S - N -
176 Agrotis subterranea (F.)	U	- - M - - - - - - - - -
177 Alypia wittfeldi Hy.Edw.	U	- - M - - - - - - - - -
178 Amolita fessa Grt.	U	- - - A - - - - - O - -
179 Amolita obliqua Sm.	O	J F M A - - - - - - - -
180 Anicla infecta (Ochs.)	U	- F - - - - - - - - - -
181 Anomis erosa Hbn.	U	- - - - - - - - - - N -
182 Anomis flava fimbriago (Steph.)	U	- - - - - - - - - - N -
183 Anomogyna elimata (Gn.)	U	- - - - - - - - - - N -
184 Anticarsia gemmatilis Hbn.	O	- - - - - - - - S O N D
185 Argyrogramma basigera (Wlk.)	U	- - - - M - - - - - N -
186 Argyrostrotis quadrifilaris (Hbn.)	U	- - M - M - - - - - - -
187 Arugisa ? latiorella (Wlk.)	U	- - M - - - - - - - - -
188 Bagisara repanda (F.)	U	- - - - - - - - - - - D

Table 1 (Continued)

	Abundance	Month
189 Bellura gortynoides Wlk.	U	- - - A - - - A - O - -
190 Bellura obliqua (Wlk.)	U	- F M - - - - - - - - -
191 Bleptina caradrinalis Gn.	U	- F M - - - - - - - - -
192 Bomolocha baltimoralis (Gn.)	U	- - M A - - - - - - - -
193 Caenurgia chloropha (Hbn.)	U	J - M - - - - - - - - -
194 Callopistria cordata (Ljungh)	U	- - - A - - - - - - - -
195 Callopistria granitosa (Gn.)	U	- - - - - - - - S - - -
196 Callopistria mollissima (Gn.)	U	- - - A M - - - - - - -
197 ? Catocala amica (Hbn.)	O	- - - - - J - - - - - -
198 Catocala andromedae Gn.	A	- - - - M - - - - - - -
199 Catocala cara Gn.	U	- - - - - J - - - - - -
200 Catocala clintonii Grt.	U	- - - A M - - - - - - -
201 Catocala connubialis Gn.	U	- - - - M - - - - - - -
202 Catocala consors (J.E.Smith)	U	- - - - - J - - - - - -
203 Catocala ilia (Cram.)	A	- - - - M J - - - - - -
204 Catocala jair Stkr.	U	- - - - - J - - - - - -
205 Catocala louiseae J.Bauer	C	- - - - M - - - - - - -
206 Catocala micronympha Gn.	O	- - - - M J - - - - - -
207 Catocala muliercula Gn.	C	- - - - M J - - - - - -
208 Catocala similis Edw.	A	- - - - M - - - - - - -
209 Catocala ultronia (Hbn.)	C	- - - - M - - - - - - -
210 Chaetaglaea tremula (Harv.)	O	J F - - - - - - - - - D
211 Charadra deridens (Gn.)	O	- F M - - J J - S - - -
212 Cissusa spadix (Cram.)	O	- F M A - - - - - - - -
213 Copipanolis styracis (Gn.)	A	J F - - - - - - - - - -
214 Cryphia nanoides Franc.& Todd	C	- - M A M - - - - O - -
215 Cutina albopunctella Wlk.	U	- - M - - - - - - - - -
216 Cutina distincta (Grt.)	U	- - M - - - - - - - - -
217 Cutina sp.	O	- F - A - - - - - - - -
218 Cutina sp.	O	- F - - - - - - - - - -
219 Derrima stellata Wlk.	U	- - - - - - - - S - - -
220 Dyspyralis n. sp.?	U	J - - - - - - - - O - -
221 Egira alternans (Wlk.)	U	- - M - - - - - - - - -
222 Elaphria chalcedonia (Hbn.)	U	- - - A - - - - - O - D
223 Elaphria exesa (Gn.)	U	- - M - - - - - - - - -
224 Elaphria festivoides (Gn.)	C	- - M A - - - - - - N D
225 Elaphria versicolor (Grt.)	O	- F - - - - - - - - - D
226 Epidromia fergusoni Solis	U	- - - - - - - - - O - -
227 Euclida cuspidea (Hbn.)	U	- - - A - - - - - - - -
228 Eucoptocnemis dapsilis (Grt.)	U	- - - - - - - - - - N -
229 Eudryas grata (F.)	U	- - - - - J - - - - - -
230 Eudryas unio (Hbn.)	U	- - M - - - - - - - - -

Table 1 (Continued)

		Abundance	Month
231	Eumicremma minima (Gn.)	U	- - - - - - - - S O - -
232	Eutolype rolandi Grt.	U	- - M - - - - - - - - -
233	Feltia geniculata G.& R.	U	- - - - - - - - - O N -
234	Galgula partita Gn.	U	- F M - - - - - - - - -
235	Harrisimemma trisignata (Wlk.)	U	- - - - - - - - S - - -
236	Heliothis turbatus (Wlk.)	U	- - - - - - - - - O - -
237	Heliothis virescens (F.)	U	- - - A - - - - S - - -
238	Hemeroplanis habitalis (Wlk.)	C	- - M - - - J - - - - -
239	Himella intractata (Morr.)	U	- - M - - - - - - - - -
240	Homophoberia cristata Morr.	U	- - - A - - - - - - - -
241	Hormisa orciferalis Wlk.	U	- F M - - - J A - - - -
242	Hormoschista latipalpis (Wlk.)	O	- - - A - - - A S - N -
243	Hypenula cacuminalis (Wlk.)	U	- - - A M - - - - - - -
244	Hypsoropha hormos Hbn.	O	- - M - M - - - - - - -
245	Hypsoropha monilis (F.)	U	- - M - - - - - - - - -
246	Idia aemula Hbn.	O	J - M - - - - - - - - -
247	Idia americalis (Gn.)	U	- - - A - - - - - - - -
248	Idia lubricalis (Gey.)	C	- - - - M - - - - - - -
249	Iodopepla u-album (Gn.)	U	J - - - - - - - - - - -
250	Isogona tenuis (Grt.)	U	- - - - - - - A - - - -
251	Lacinipolia laudabilis (Gn.)	O	J F M A - - - - - O - -
252	Lascoria ambigualis Wlk.	U	- F - - - - - - - - - -
253	Ledaea perditalis (Wlk.)	O	- F M A - - - - - - - -
254	Lesmone detrahens (Wlk.)	U	- - - A - - - - - - - -
255	Lesmone hinna (Gey.)	U	- - - - M - - - - - N -
256	Leucania scirpicola Gn.	U	- F - A - - - - - - - -
257	Lithophane looks like innominata (Smith)	U	J - - - - - - - - - - -
258	Lithophane viridipallens Grt.	U	J - - - - - - - - - - -
259	Lithophane sp.	U	- F - - - - - - - - - -
260	Litoprosopus futilis (Grt. & Rob.)	U	- - - - - J - - - - - -
261	Marathyssa basalis Wlk.	O	J - M - - - - - - - - -
262	Marathyssa inficita (Wlk.)	O	- - M A M - - - - - - -
263	Meganola minuscula (Zell.)	O	- F - - M - - - - O - -
264	Melipotis jucunda Hbn.	O	- - - A M - - - - - - -
265	Meropleon cosmion Dyar	U	- - - - - - - - - - N D
266	Metalectra quadrisignata (Wlk.)	U	- - M - - - - - - - - -
267	Metalectra sp.	U	- - - - M - - - - - - -
268	Metria amella (Gn.)	U	- - M A - - - - - - - -
269	Mocis disseverans (Wlk.)	O	- - - - - - - - - O - -
270	Mocis latipes (Gn.)	C	- - - - - - - - - O - -
271	Mocis marcida (Gn.)	U	- F - - - - - - - - - -
272	Mocis texana (Morr.)	U	- - - - - - - - - O - -
273	Morrisonia confusa (Hbn.)	C	- - M A - - - - - - - -

Table 1 (Continued)

	Abundance	Month
274 Morrisonia mucens (Hbn.)	A	- F M A - - - - - - - -
275 Nigetia formosalis Wlk.	C	- F M A M - - - S O - -
276 Nola sorghiella Riley	U	- - - - - - - A S - - -
277 Ogdoconta cinereola (Gn.)	U	- - M - - - - - - - - -
278 Oligia fractilinea (Grt.)	U	- - - - - - - - - O - -
279 Ophiuche minualis (Gn.)	U	- - - - - - - - - - N -
280 Oruza albocostaliata (Pack.)	O	- - - A - J J - - - - -
281 Oxycilla prob. mitographa (Grt.)	U	- - - - - - - - S - - -
282 Paectes abrostoloides (Gn.)	U	- - - - - - - - S - - -
283 Palthis angulalis (Hbn.)	U	- - - A - - - - - O - -
284 Palthis asopialis (Gn.)	U	J F - - M - - - - - - D
285 Pangrapta decoralis Hbn.	O	- - M A M - - - - - - -
286 Panopoda repanda (Wlk.)	U	- - M - - - - - - - - -
287 Panopoda rufimargo (Hbn.)	U	- - - - M - - - - - - -
288 Panthea furcilla (Pack.)	C	J - M - - - - - - - N D
289 Parallelia bistriaris Hbn.	U	- - - - M - - - S - - -
290 Phalaenostola larentioides Grt.	U	- - - A - - - - - - - -
291 Phoberia atomaris Hbn.	O	- - M - - - - - - - - -
292 Phosphila miseloides (Gn.)	U	- F M - - - - - - - N -
293 Phosphila turbulenta Hbn.	O	- F - - - - - - S O - -
294 Phyprosopus callitrichoides Grt.	U	- F - - M - - - - - - -
295 Phytometra rhodarialis (Wlk.)	U	- - M - - J - - - - - -
296 Plathypena scabra (F.)	U	- F - - - - - - - - - -
297 Platysenta mobilis (Wlk.)	U	- - - - - - - - - - - D
298 Platysenta sutor (Gn.)	O	- F - - - J - - - - N D
299 Platysenta videns (Gn.)	U	- - M - - - - - - - - -
300 Polygrammate hebraeicum Hbn.	O	- - - - - - - A - - - -
301 Proroblemma testa B.& McD.	O	- - - A - J - - - - N D
302 Psaphidia resumens Wlk.	U	J F - - - - - - - - - -
303 Pseudanthracia coracias (Gn.)	U	- F - - - - - - - - - -
304 Pseudoplusia includens (Wlk.)	O	J - - - - - - - - O - D
305 Ptichodis herbarum (Gn.)	U	- - - - M - J - S - - -
306 Ptichodis vinculum (Gn.)	U	- - - A M - - - - - - -
307 Redectis vitrea (Grt.)	U	- - - A - - - - - - - -
308 Renia salusalis (Wlk.)	U	- F M - - - - - - - - -
309 Schinia bina (Gn.)	U	- - - - - - - - S - - -
310 Schinia gaurae (J.E.Smith)	U	- - - - M - - - - - - -
311 Schinia nubila (Stkr.)	U	- - - - - - - - S - - -
312 Schinia nundina (Drury)	U	- - - - - - - - S - - -
313 Schinia rivulosa (Gn.)	U	- - - - - - - - S - - -
314 Schinia saturata (Grt.)	C	- - - - - - - A S O - -
315 Schinia scissoides (Benj.)	U	- - - - - - - - - O - -
316 Schinia siren (Stkr.)	U	- - - - - - - - S - - -

Table 1 (Continued)

	Abundance	Month
317 Schinia trifascia Hbn.	O	- - - - - - - - S O N -
318 Schinia tuberculum (Hbn.)	U	- - - - - - - - - O - -
319 Scolecocampa liburna (Gey.)	U	- - M - M - - - - - - -
320 Selenisa sueroides (Gn.)	O	- - - - - - - - - O - D
321 Sigela prob. eoides (B.& McD.)	U	- F - - - - - - - - - D
322 Spodoptera eridania (Cram.)	U	- - - - - J - - - O - -
323 Spodoptera latifascia (Wlk.)	O	- - - - M - - - - - N D
324 Spragueia onagrus (Gn.)	C	- - - A - J J - S - - -
325 Tarachidia candefacta (Hbn.)	O	- - M - - - - A S - - -
326 Tarachidia semiflava (Gn.)	U	- - - - M J - - S - - -
327 Thioptera nigrofimbria (Gn.)	U	- - M A - - - - S - - -
328 Trichoclea vindemialis (Gn.)	U	- - M - - - - - - - - -
329 Xystopeplus rufago (Hbn.)	U	- F - - - - - - - - - -
330 Zale aeruginosa (Gn.)	C	J F M - M J - - - - - -
331 Zale buchholzi McD.	C	J F M - - - - - - - N -
332 Zale declarans (Wlk.)	C	- F M A - - - - - - - -
333 Zale horrida Hbn.	U	- - M - - - - - - - - -
334 Zale lunata (Drury)	O	- - - - M J - - - - - -
335 Zale lunifera (Hbn.)	O	- F M - - - - - - - - -
336 Zanclognantha minoralis Sm.	U	- F - - - - - - - - - -
337 ? Cyathissa n. sp.	C	- F M A - - - A S O N -
NOTODONTIDAE		
338 Dasylophia anguina (J.E.Smith)	O	- F M A - - - - S - - -
339 Datana angusii G.& R.	O	- - - - - - - - S - - -
340 Datana integerrima G. & R.	U	- - - - M - - - - - - -
341 Datana major G.& R.	O	- - - - - J J A S - - -
342 Datana modesta Beutenmuller	U	no date
343 Datana near ranaeceps (Guer.-Meneville)	U	- - - - - - - A - - - -
344 Datana robusta Stkr.	U	- - - - - - - A - - - -
345 Furcula cinerea (Wlk.)	U	- - - - - - - - S - - -
346 Heterocampa astarte Doubleday	U	- - M A - - - A - - - -
347 Heterocampa biundata Wlk.	O	- F - A - - - - - O N -
348 Heterocampa umbrata Wlk.	O	- - M A - - - - - - - D
349 Heterocampa varia Wlk.	O	- - - A - - - A S - - -
350 Hyparpax perophoroides (Stkr.)	U	- F - A - - - - - - - -
351 Hyperaeschra georgica (H.-S.)	U	- - M A - - - A - - - -
352 Lochmaeus bilineata (Pack.)	U	- F - - - - - - - - - -
353 Lochmaeus manteo Doubleday	U	- - - - - - J - - - - -
354 Macrurocampa marthesia (Cram.)	O	- - - - - - - - S O N D
355 Nadata gibbosa (J.E.Smith)	C	- F M - - J J - S - - -
356 Oligocentria lignicolor (Wlk.)	U	- - - - - - - - S - - -
357 Peridea angulosa (J.E.Smith)	U	J - - - - - - - - - N -
358 Schizura ipomoeae Doubleday	U	- - - - - - - - S O - -

Table 1 (Continued)

	Abundance	Month
359 Schizura unicornis (J.E.Smith)	O	- - M A - - - - - - N -
360 Symmerista albifrons (J.E.Smith)	O	J F - - - - - - - - - -
OECOPHORIDAE		
361 Antaeotricha leucillana (Zell.)	A	J F M A - - - - - O - D
362 Antaeotricha osseella (Wlsm.)	U	- - - - - - - - - O - -
363 Antaeotricha vestalis (Zell.)	C	- - - - M - - A S - - -
364 Callima nathrax Hodges	O	- - - - - - - - S - - -
365 Decantha boreasella (Cham.)	O	- F - - - - - - - - - -
366 Inga sparsiciliella (Clem.)	C	- - - A - - J - - - - -
PLUTELLIDAE		
367 Plutella xylostella (L.)	O	- - - - - - - - - O - -
PSYCHIDAE		
368 Cryptothelea gloverii (Pack.)	O	- - - - M - - - - O - -
369 Thyridopteryx ephemeraeformis (Haw.)	C	- - - - - - J - - - - -
PTEROPHORIDAE		
370 Geina ? periscelidactyla (Fitch)	U	- - - - - - - - - - - D
371 Oidaemotophorus balanotes (Meyr.)	A	- - M - - - - - S O N D
372 Stenoptilia parva Wlsm.	U	- - - - - - - - - - N -
PYRALIDAE		
373 Acrobasis grossbecki (B.& McD.)	U	- - - - M - - - - - - -
374 Adelphia petrella (Zell.)	O	- F M - - - - - - - - -
375 Aglossa cuprina Zell.	U	- - - A - - - - - - - -
376 Anageshna primordialis (Dyar)	O	- - M - - - - - - - - -
377 Apogeshna stenialis (Gn.)	U	- - M - - - J - S - - -
378 Argyria lacteella (F.)	O	J - - - - - - - - O - -
379 Arta sp.	U	- - - - - - - - - O - -
380 Atheloca subrufella (Hulst)	U	J - - - - - - - - - - -
381 Basacallis tarachodes Dyar	O	J - M - - - - - - - - D
382 Blepharomastix ranalis (Gn.)	O	- - - A M - - - - - - -
383 Chrysendeton imitabilis (Dyar)	U	- - - A - - - - - - - -
384 Clydonopteron tecomae Riley	U	- - - - - - - - - - - D
385 Conchylodes concinnalis Hamp.	O	- - - - - - J A S - - -
386 Crambus praefectellus (Zinck.)	U	- - - A M - - - - - - -
387 Crambus quinquareatus Zell.	U	- - M - - - - - S - - -
388 Crambus sanfordellus Klots	O	- - M - - - - - - - - D
389 Crambus satrapellus (Zinck.)	C	J F M A M - - - - O - D
390 Desmia funeralis (Hbn.)	O	- F M - M - - - - - - -
391 Diacme ? adipaloides (G.& R.)	U	J F - - - - - - - - N -
392 Diasemiopsis leodocusalis (Wlk.)	U	- - - - - - - - - O - -
393 Diatraea lisetta (Dyar)	U	- - - - - - - - - O - -
394 Dicymolomia julianalis (Wlk.)	O	- - M A - - - - - - - -
395 Dioryctria abietivorella (Grt.)	U	- - M - - - - - - - - -
396 Dioryctria amatella (Hulst)	C	- - - A M - - - - O N -

Table 1 (Continued)

		Abundance	Month
397	Dioryctria clarioralis (Wlk.)	O	- - M A M - J - - - - -
398	Donacaula maximella (Fern.)	O	- - - A M - - - - - - -
399	Donacaula prob. melinella (Clem.)	U	- - - - - - - - S - - -
400	Donacaula nitidella (Dyar)	U	- - M A - - J - - - - -
401	Donacaula roscidella (Dyar)	U	- - - - M - - - S O - -
402	Donacaula sordidella (Zinck.)	U	- - - A - - - - - - - -
403	Elasmopalpus lignosellus (Zell.)	U	- - - - - - - - - - N D
404	Eoparargyractis irroratalis (Dyar)	C	- - - A - - - - - O N -
405	Epipagis huronalis (Gn.)	U	- - - - - - - - - O N -
406	Epipaschia superatalis Clem.	U	- - - - M - - - - - - -
407	Eudonia strigalis (Dyar)	O	J F - - - - - - - - N -
408	Eustixia pupula Hbn.	U	- - - A - - - - - - - -
409	Fissicrambus ?hemiochrellus (Zell.)	O	J - - A - - - - - O N -
410	Fissicrambus mutabilis (Clem.)	U	- - - - - - - - - O - -
411	Galasa nigrinodis (Zell.)	U	- - - A - - - - - - - -
412	Glaphyria basiflavalis B.& McD.	U	- - M - - - - - - - - -
413	Glaphyria fulminalis (Led.)	U	- - - A - - - A - - - -
414	Glaphyria glaphyralis (Gn.)	U	- - - A M - - - - - - -
415	Glaphyria sesquistrialis Hbn.	U	- - - - M - - - - - - -
416	Glyphodes sibillalis Wlk.	U	- - - - - - - - S O - -
417	? Hahncappsia mancalis (Led.)	U	- - - - M - - - - - - -
418	Hellula rogatalis (Hulst)	U	- F - A - - - - - - - -
419	Herculia binodulalis (Zell.)	O	- - - A - - - - - - N -
420	Herculia sordidalis B.& McD.	U	- - - - - - - - - - N -
421	Hydriris ornatalis (Dup.)	U	- - - - - - - - - - N -
422	Hymenia perspectalis (Hbn.)	U	- - - - - - - - - - N D
423	Jocara incrustalis (Hulst)	O	J F - - M - - A S - - -
424	Laetilia coccidivora (J.H.Comstock)	U	- F - - - - - - - - - D
425	Lepidomys irrenosa Gn.	C	- - M A M - - A S - - -
426	Lineodes fontella Wlsm.	U	- - - - - J - - S - - -
427	Lipocosmodes fuliginosalis (Fern.)	U	- - - - - - - - S - - -
428	Marasmia cochrusalis (Wlk.)	U	- F - - - - - - - - - -
429	Melitara prodenialis Wlk.	U	- - - A - - - - - O - -
430	Mesolia incertella (Zinck.)	U	- - - - - - - - - O - -
431	Microcausta flavipunctalis B.+McD.	U	- F M - - - - - - - - -
432	Microcrambus biguttellus (Fbs.)	U	no date
433	Microcrambus elegans (Clem.)	C	- - M A M - - - - - - -
434	Microtheoris ophionalis (Wlk.)	U	- - - - - J - - - - - -
435	Moodna ostrinella (Clem.)	C	J F M A - - - - - - - D
436	Munroessa gyralis (Hulst)	U	- - - - - - - A - O - -
437	Munroessa icciusalis (Wlk.)	U	- - - - - - - - - - N -
438	Munroessa nebulosalis (Fern.)	U	- - - - - - - - - O - -
439	Neargyractis slossonalis (Dyar)	U	- - - - - - - - - - N -

Table 1 (Continued)

	Abundance	Month
440 Nomophila nearctica Mun.	U	- - - - - - - - S - - -
441 Oenobotys vinotinctalis (Hamp.)	U	- - M - - - - - - - - -
442 Omphalocera munroei Martin	U	- - - - M - - - S - - -
443 Palpita magniferalis (Wlk.)	U	J - - A - - - A - O - -
444 Palpita cincinnatalis Mun.	U	- F M - - - - - - - - -
445 Parachma ochracealis Wlk.	O	- - - A - - - A S - - -
446 Parapediasia decorella (Zinck.)	U	- - - - - - - A - O - -
447 Paraponyx allionealis Wlk.	C	- F - A - J - - - - - D
448 Paraponyx obscuralis (Grt.)	U	- - - - - - - - - - - D
449 Peoria approximella (Wlk.)	U	- - - - - - - - S - - -
450 Phycitinae (sp.?)	U	- - - - - - - - - O - -
451 Pleuroptya penumbralis (Grt.)	U	- - - - - - - - - - N -
452 Prionapteryx achatina Zell.	U	- - - - - J - - - O - -
453 Prionapteryx serpentella (Kft.)	U	- - - - - J - - - - - -
454 Pyrausta tyralis (Gn.)	O	- F - - - - - A - O N -
455 Raphiptera argillaceella mimimella (Rob.)	O	- F M A - - - - - - N -
456 Salebriaria fructetella (Hulst)	U	- - - - M - - - - - - -
457 Samea ecclesialis Gn.	C	J - - - - - - - - - N D
458 Samea multiplicalis (Gn.)	A	- - - - - - - - - - N D
459 Scirpophaga perstrialis (Hbn.)	U	- - - - - - - - S - - -
460 Synclita obliteralis (Wlk.)	O	- - - - - - - - - O - D
461 Synclita tinealis Mun.	U	- - - - - - - - - - N -
462 Tampa dimediatella Rag.	U	- - - A - - - - - - - -
463 Tetralopha melanogrammos Zell.	C	- F M A M - - A - - - -
464 Tetralopha robustella Zell.	O	- - - A M J - A - O - -
465 Tetralopha scortealis (Led.)	O	- - M A - - - - - - - -
466 Thaumatopsis edonis (Grt.)	O	- - - - - - - - - O N -
467 Tulsa finitella (Wlk.)	U	J - - - - - - - - - - -
468 Ufa rubedinella (Zell.)	C	- - M - - - - - - O N D
469 Uresiphita reversalis (Gn.)	U	- - - - - - - - - O - -
470 Urola nivalis (Drury)	C	J F M A - - - - - - N -
471 Xanthophysa psychialis (Hulst)	U	- - - - - J - - - - - -
472 Xubida linearella (Zell.)	O	- - M A - J - - - - - -
SATURNIIDAE		
473 Actias luna (L.)	C	- - M - - - - A - - - -
474 Anisota consularis Dyar	U	- - - - - - - A - - - -
475 Anisota virginiensis pellucida (J.E.Smith)	A	- - - - - J - A S - - -
476 Antheraea polyphemus (Cram.)	C	- - - - - - - - - O - -
477 Automeris io (F.)	A	- - - - - J - A S O - -
478 Citheronia regalis (F.)	U	- - - - - - - A - - - -
479 Dryocampa rubicunda (F.)	A	- - - - M - J A S - - -
480 Eacles imperialis Drury	C	- - - - - - - A S - - -
481 Hemileuca maia (Drury)	O	J - - - - - - - - - - -

Table 1 (Continued)

	Abundance	Month
SCYTHRIDIDAE		
482 Scythris n. sp.	U	- - - - - - - - - 0 - -
483 Scythris sp.	U	- - - - - - - - - - - D
SESIIDAE		
484 Carmenta texana (Hy.Edw.)	U	- - - - - - - - S 0 - -
485 Synanthedon alleri (Engelh.)	U	- - - - - - - - - 0 - -
486 Synanthedon exitiosa (Say)	A	- - - - - - - - S 0 - -
487 Synanthedon sapygaeformis (Wlk.)	A	- - - - - - - - S 0 - -
SPHINGIDAE		
488 Ceratomia catalpae (Bdv.)	U	- - - - - - - A - - - -
489 Darapsa myron (Cram.)	C	- - M A - - - - S - - -
490 Deidamia inscripta (Harr.)	C	- - M A - - - - - - - -
491 Dolba hyloeus (Orury)	0	- - - A - J - - - - - -
492 Enyo lugubris (L.)	C	- - - - - - - - - 0 - -
493 Eumorpha fasciatus (Sulz)	U	- - - - M - - - - - - -
494 Laothoe juglandis (J.E.Smith)	C	- - M - - - - - S - - -
495 Lapara coniferarum (J.E.Smith)	0	- - - A - J - - S - - -
496 Paonias excaecatus (J.E.Smith)	U	- - - - - - - A S - - -
497 Xylophanes tersa (L.)	0	- - - - - - - - - 0 - -
TINEIDAE		
498 Acrolophus arcanella (Clem.)	U	- - - - - - - - S - - -
499 Acrolophus plumifrontella (Clem.)	C	- - - - - J - - - - - -
500 Acrolophus propinquus (Wlsm.)	U	- - - - - J - - S - - -
501 Acrolophus texanella (Cham.)	U	- - - A - - - - - - - D
502 Acrolophus near variabilis (Wlsm.)	U	- - - - - J - - - - - -
503 Acrolophus sp.	0	- - M - - - - - - - - -
504 Acrolophus n. sp.	U	- - - - M - - - - - - -
505 Nemapogon rileyi (Dietz)	C	- F - A - - - - - - N -
506 Phereoeca walsinghami (Busk.)	C	no date
507 Tinea apicimaculella Cham.	U	- F - - - - - - - - - -
508 Xylesthia pruniramiella Clem.	U	- F - A - - - - - - - -
509 sp.	U	- - M - - - - - - - - -
510 sp.	U	- - - - - - - - - - N -
511 sp.	U	J - M - - - - - - - - D
TORTRICIDAE		
512 Amorbia humerosana Clem.	A	- - - - - J - - - 0 N D
513 Ancylis comptana (Frolich)	0	- F - - M - - - - - - D
514 Archips argyrospila (Wlk.)	A	- - - A M - - - - - - -
515 Archips georgiana (Wlk.)	A	- - - A M - - - - - - -
516 Archips ? grisea (Rob.)	U	- - - A - - - - - - - -
517 Archips infumatana (Zell.)	U	- - - - M - - - - - - -
518 Archips semiferana (Wlk.)	A	- - - A M - - - - - - -
519 Argyrotaenia n. sp.	0	- F - - - - - - - - - D

Table 1 (Continued)

	Abundance	Month
520 Argyrotaenia ivana (Fern.)	U	- F - - - - - - - - - -
521 Argyrotaenia quercifoliana (Fitch)	C	- - - A M - - - - - - -
522 Argyrotaenia tabulana Free.	A	J F M A - - - - S O - D
523 Cacocharis cymotoma (Meyr.)	U	- - M - - - - - - - N -
524 Chimoptesis pennsylvaniana (Kft.)	A	J F M - - - - - - - - -
525 Chimoptesis n. sp.	C	- F M - - - - - - - - -
526 Choristoneura obsoletana (Wlk.)	U	- - - - - - - - S - - -
527 Choristoneura rosaceana (Harr.)	A	- F - A M - - - - - - -
528 Coelostathma discopunctana Clem.	O	- F M - - - - - - - - -
529 Crocidosema plebejana Zell.	U	J F M - - - - - - - - -
530 Croesia semipurpurana (Kft.)	A	- - - A M - - - - - - -
531 Cydia ingens (Heinr.)	U	- - - A M - - - - - - -
532 Cydia n. sp.	O	- F - - - - - - - - - -
533 Cydia n. sp.	O	J F M - - - - - - - - -
534 Cydia n. sp.	U	- F - - - - - - - - - -
535 Ecdytolopha punctidiscanum (Dyar)	U	- - - - M - - - - O - -
536 Endopiza prob. liriodendrana (Kft.)	O	- F M - - - - - - - - -
537 Endopiza spiraeifoliana (Heinr.)	U	- - M - - - - - - - - -
538 Endothenia hebesana (Wlk.)	U	- - - A - - - - - - - -
539 Epiblema scudderiana (Clem.)	O	- - M A M J - - - - - -
540 Epiblema strenuana (Wlk.)	U	- - M A - - - - - - - -
541 ? Epiblema sp.	U	- - - - - - - - - O - -
542 ? Epinotia sp.	U	- F - - - - - - - - - -
543 Episimus argutanus (Clem.)	U	- - - A - - - - - - - -
544 Episimus tyrius Heinr.	U	- F M A M - - - - - - -
545 Eucosma adamantana (Gn.)	C	- - - - - - - - - - N D
546 Eucosma circulana Hbn.	U	J - - - - - - - - - - -
547 Eucosma cocana Kft.	A	- F M A M - - - - - - -
548 Eucosma gigantica (Riley)	U	- - - - - J - - - - - -
549 Eucosma guttalana Blanchard	O	- - - - M - - A S - N -
550 Eucosma robinsonana (Grt.)	A	- - M A M - J - - - - -
551 ? Eucosma n. sp.	O	J F M - - - - - - - - -
552 Eumarozia malachitana (Zell.)	O	- F - - - - - - - O N -
553 Gretchena bolliana (Slingerland)	O	- F - A M - - - S - - D
554 Melissopus latiferreanus (Wlsm.)	O	- - - - - - - A - O N -
555 ?Olethreutes devotana Kft.	?	- - M - - - - - - - - -
556 Olethreutes near hippocastana (Kft.)	U	- - - - - - - - - O - -
557 Petrova gemistrigulana (Kft.)	C	- - - A M - - - - - - -
558 Phaecasiophora niveiguttana (Grt.)	O	- - M A - - - - - - - -
559 Phaneta ?argutipunctana Blanch. & Knudson	O	- - - - - - - - S - - -
560 Phaneta raracana (Kft.)	O	- - M - - - - - S O - -
561 Phaneta sp.	U	J - - - - - - - S - - D
562 ? Phaneta sp.	U	- - - - - - - - - - - D

Table 1 (Continued)

		Abundance	Month
563	Platynota exasperatana (Zell.)	C	J F M - - - - - - - O - -
564	Platynota flavedana Clem.	A	J F M A M - - - S O N D
565	Platynota idaeusalis (Wlk.)	U	- - M - - - - - - - - -
566	Platynota rostrana (Wlk.)	U	- F - - - - - - - - - -
567	Pseudexentera haracana (Kft.)	U	- F M - - - - - - - - -
568	Pseudexentera spoliana (Clem.)	U	- F - - - - - - - - - -
569	Pseudexentera sp.	O	- F M - - - - - - - - -
570	Pseudogalleria inimicella (Zell.)	O	- - M A - - - - - O - -
571	Ptycholoma peritana (Clem.)	C	- F M A - - - - - - N D
572	Rhopobota near finitimana Heinr.	C	- F M - - - - - S - - -
573	Rhyacionia busckana Heinr.	C	- F - - - - - - - - N D
574	Rhyacionia frustrana (Comstock)	U	- F - - - - - - - - - -
575	Rhyacionia n. sp.	U	- F - - - - - - - - - -
576	Sonia constrictana (Zell.)	C	J - M A - - - - - O N -
577	Sonia sp.	U	- - - - - - - - - O - -
578	Sparganothis caryae (Rob.)	U	- - - - M J - - - - - -
579	Sparganothis n. sp.	O	no date
580	Strepsicrates smithiana (Wlsm.)	O	- - - A M - J - - - - -
581	Suleima sp.	U	- F - - - - - - - - - -
582	? Suleima sp.	A	- F M - - - - - - - - -
583	Zomaria andromedana (B.& McD.)	C	- F M - - - - - S O N -
584	Zomaria interruptolineana (Fern.)	C	- F M - - - - - S O - -
585	Zomaria rosaochreana (Kft.)	O	- - - - - - - A - O - D
586	n. sp.	U	- - - A - - - - - - - -
587	sp.	U	- - - - - - - - S - - -
YPONOMEUTIDAE			
588	Atteva punctella (Cram.)	C	- - - - M - - - S - - -
589	Urodus parvula (Hy.Edw.)	O	- F M - - - - - - - - -
ZYGAENIDAE			
590	Acoloithus falsarius Clem.	O	- - - - - - - - S O - -
DANAIDAE			
591	Danaus gilippus berenice (Cram.) Queen		
592	Danaus p. plexippus (L.) Monarch		
HESPERIIDAE			
593	Calpodes ethlius (Stoll) Brazilian Skipper		
594	Copaeodes minimus (Edw.) Southern Skipperling		
595	Epargyreus c. clarus (Cram.) Silver-spotted Skipper		
596	Erynnis horatius (Scud. & Burg.) Horaces Dusky-wing		
597	Lerema accius (J.E. Smith) Clouded Skipper		
598	Oligoria maculata (Edw.) Twin-spotted Skipper		
599	Panoquina ocola (Edw.) Ocola Skipper		
600	Polites v. vibex (Gey.) Whirlabout		
601	Urbanus p. proteus (L.) Long-tailed Skipper		

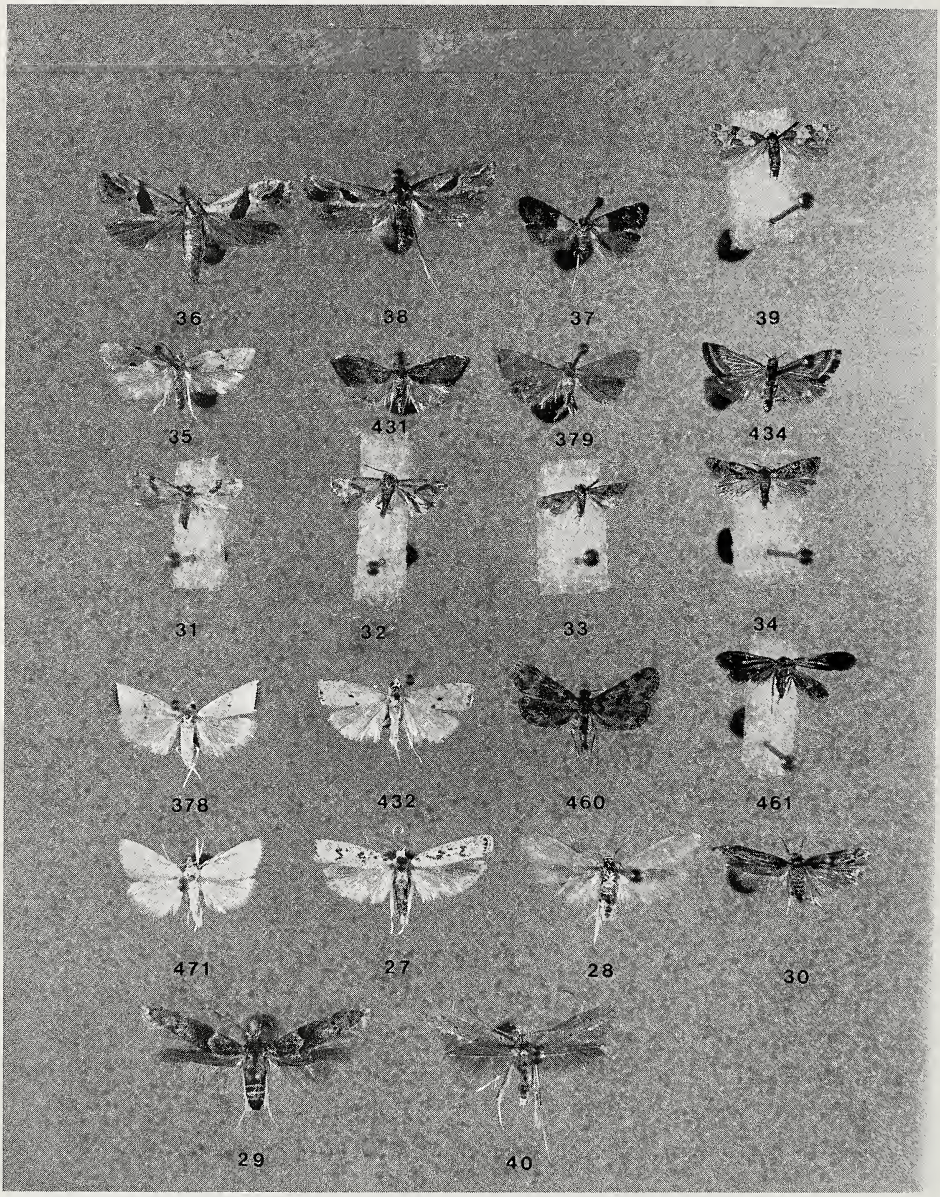
Table 1 (Continued)

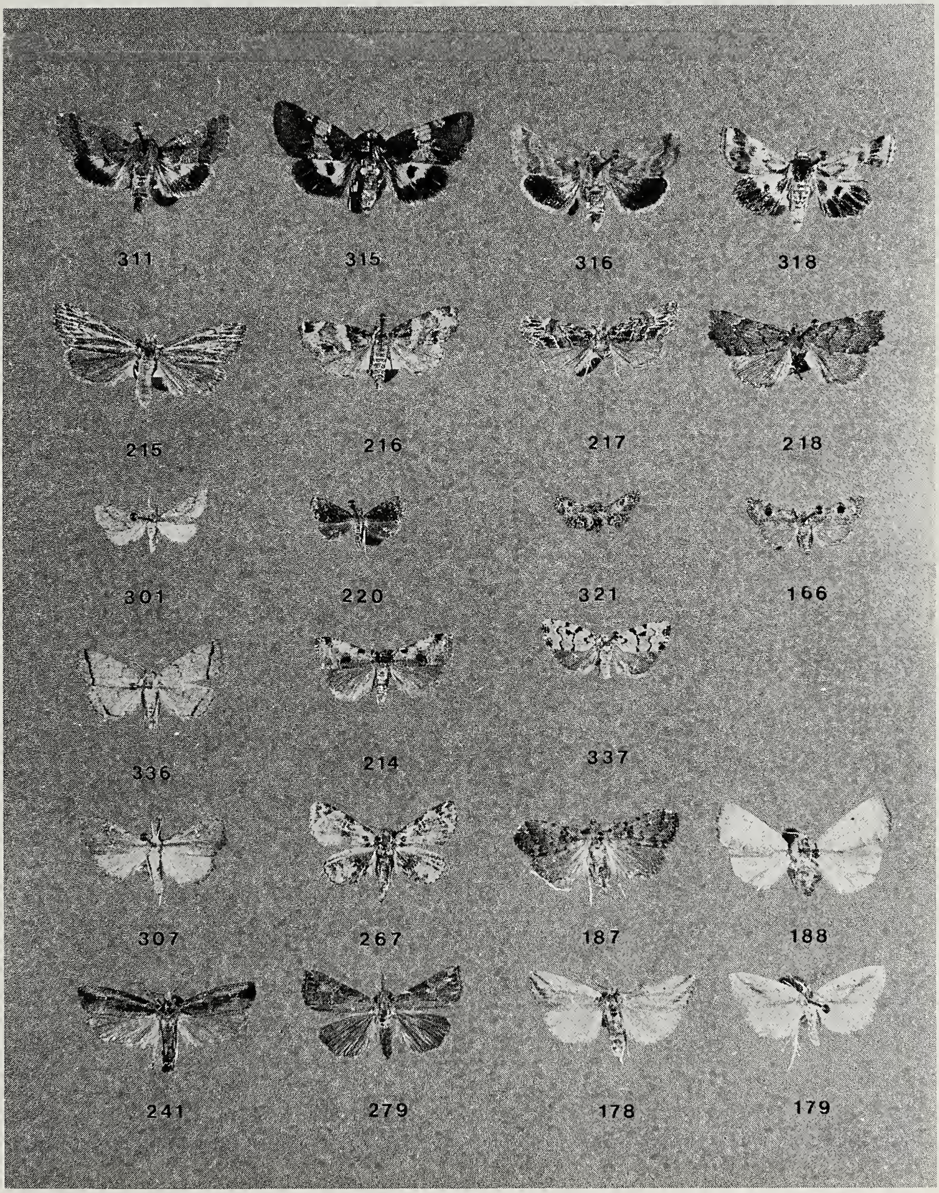
	Abundance	Month
PAPILIONIDAE		
602 Battus p. philenor (L.) Pipevine Swallowtail		
603 Eurytides marcellus (Cram.) Zebra Swallowtail		
604 Papilio c. cresphontes Cram. Giant Swallowtail		
605 Papilio glaucus australis Maynard Tiger Swallowtail		
606 Papilio palamedes Drury Palamedes Swallowtail		
607 Papilio polyxenes asterius Stoll Black Swallowtail		
608 Papilio troilus ilioneus J.E. Smith Spicebush Swallowtail		
PIERIDAE		
609 Ascia monuste phileta (F.) Great Southern White		
610 Eurema d. daira (Godt.) Barred Sulpher		
611 Eurema l. lisa Bdv. & Leconte Little Sulpher		
612 Eurema nicippe (Cram.) Sleepy Orange		
613 Phoebis sennae eubule (L.) Cloudless Sulpher		
614 Zerene c. cesonia (Stoll) Dogface Sulpher		
LYCAENIDAE		
615 Calycopis cecrops (F.) Red-banded Hairstreak		
616 Euristrymon favonius (J.E. Smith) Southern Hairstreak		
617 Hemiargus ceraunus antibubastus Hbn. Ceraunus Blue		
618 Parrhasius m-album (Bdv. & Leconte) White-m Hairstreak		
619 Strymon m. melinus Hbn. Gray Hairstreak		
NYMPHALIDAE		
620 Agraulis vanillae nigrior Michener Gulf Fritillary		
621 Anartia jatrophae guantanamo Mun. White Peacock		
622 Asterocampa celtis (Bdv. & Leconte) Hackberry Butterfly		
623 Basilarchia archippus floridensis (Stkr.) Vicery		
624 Basilarchia arthemis astyanax (F.) Red-spotted Purple		
625 Heliconius charitonius tuckeri Comstock Zebra		
626 Junonia coenia (Hbn.) Buckeye		
627 Phyciodes phaon (Edw.) Phaon Cresent		
628 Phyciodes t. tharos (Drury) Pearl Cresent		
629 Vanessa atalanta rubria (Fruhstorfer) Red Admiral		
630 Vanessa virginiensis (Drury) Am. Painted Lady		
SATYRIDAE		
631 Hermeuptychia sosybius (F.) Carolina Satyr		
632 Megisto cymela viola (Maynard) Little Wood Satyr		

additions;

633 TINEIDAE: Acrolophus sp.

In the following plates, the figure number is equivalent to the species list number for each species in table 1.

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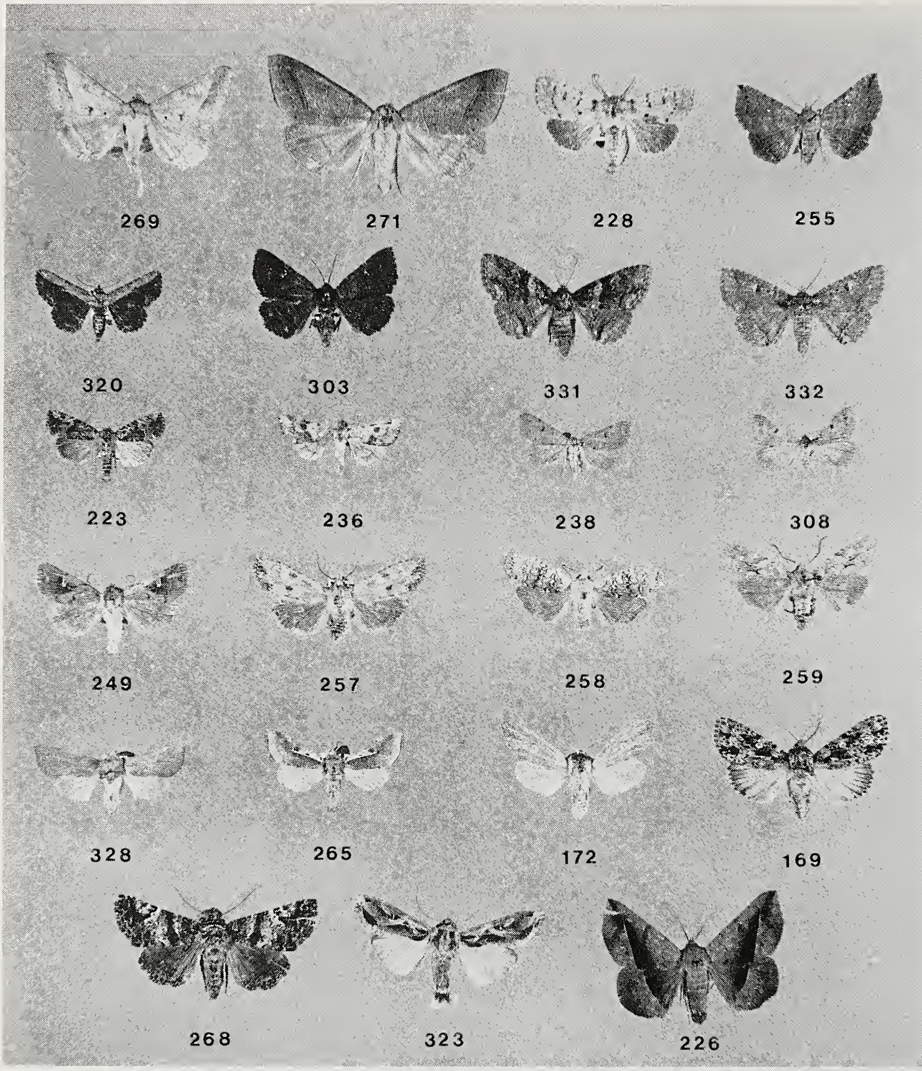
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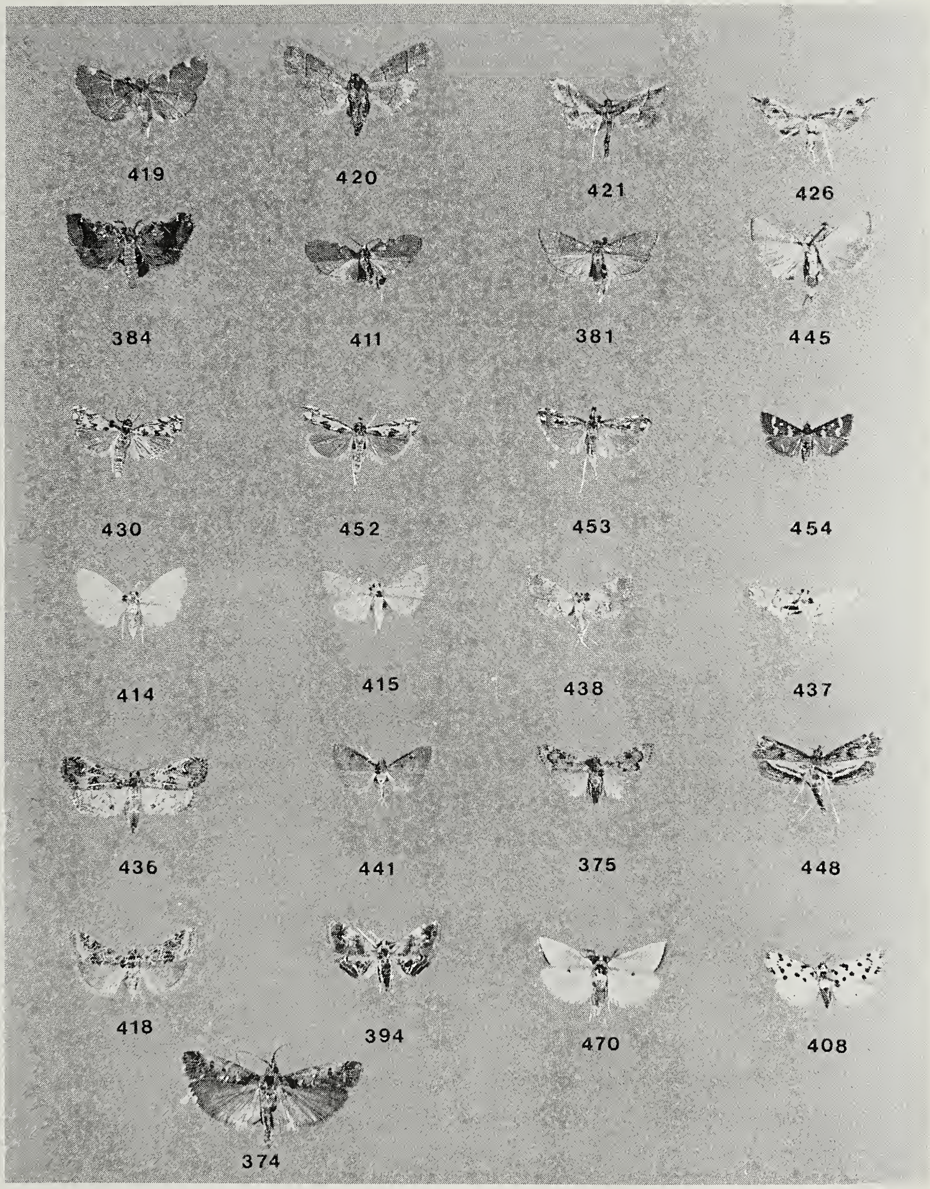
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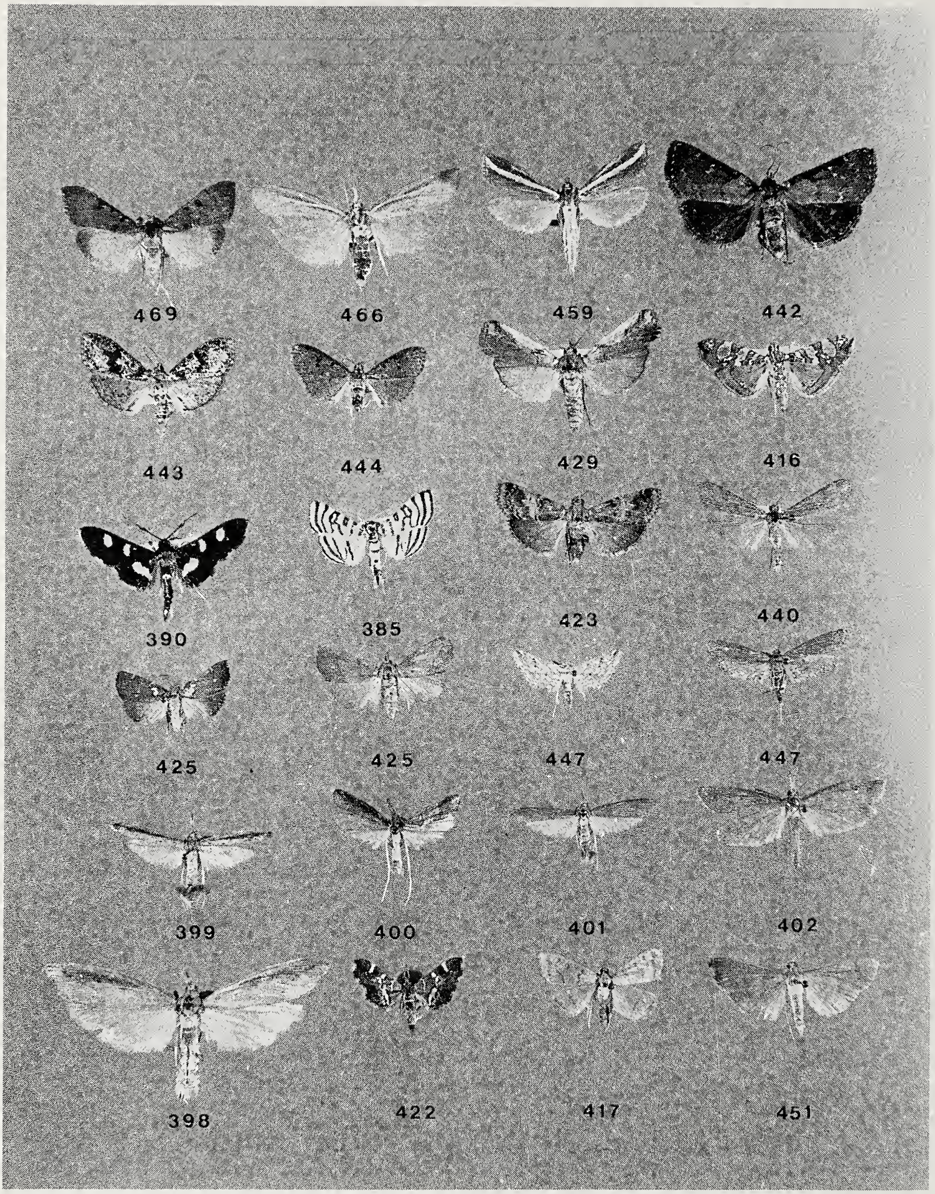
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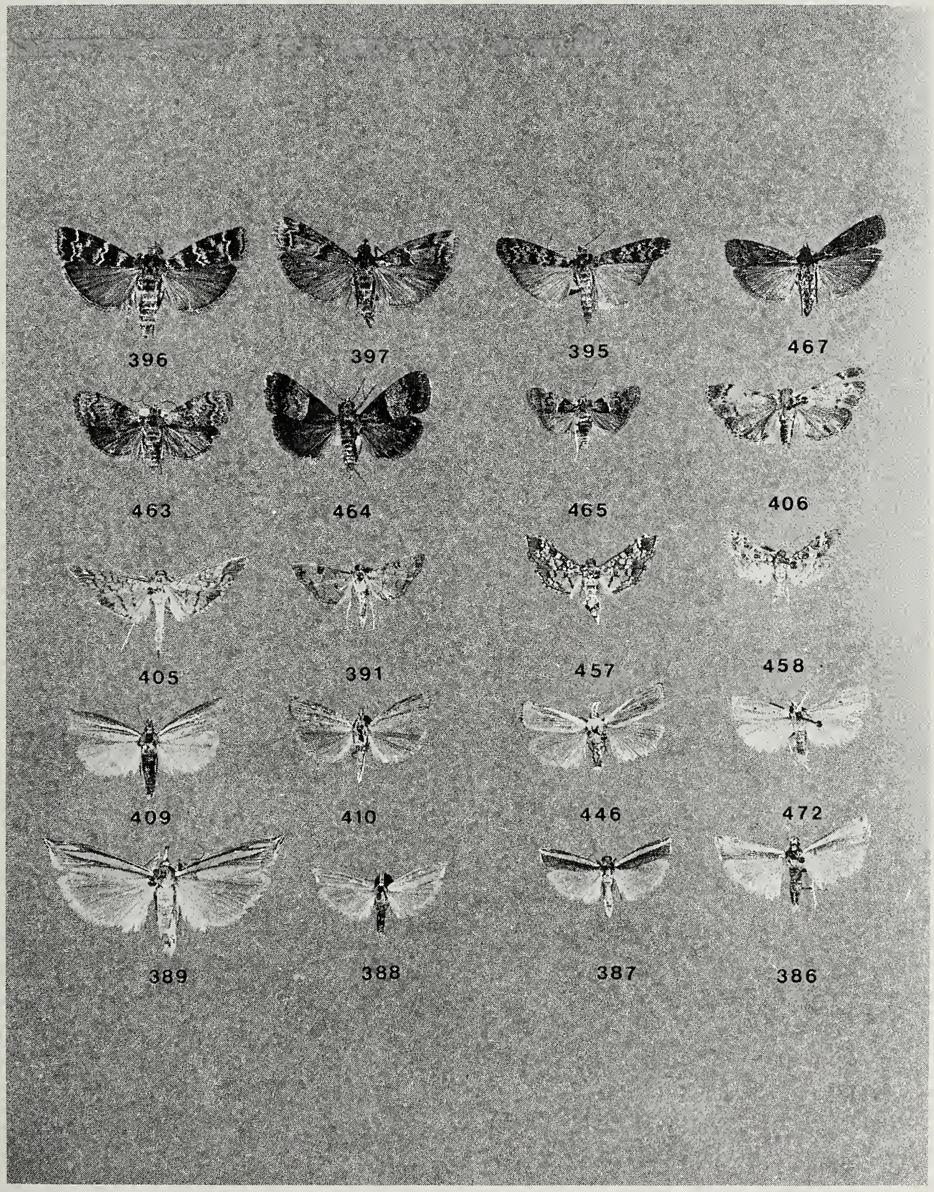
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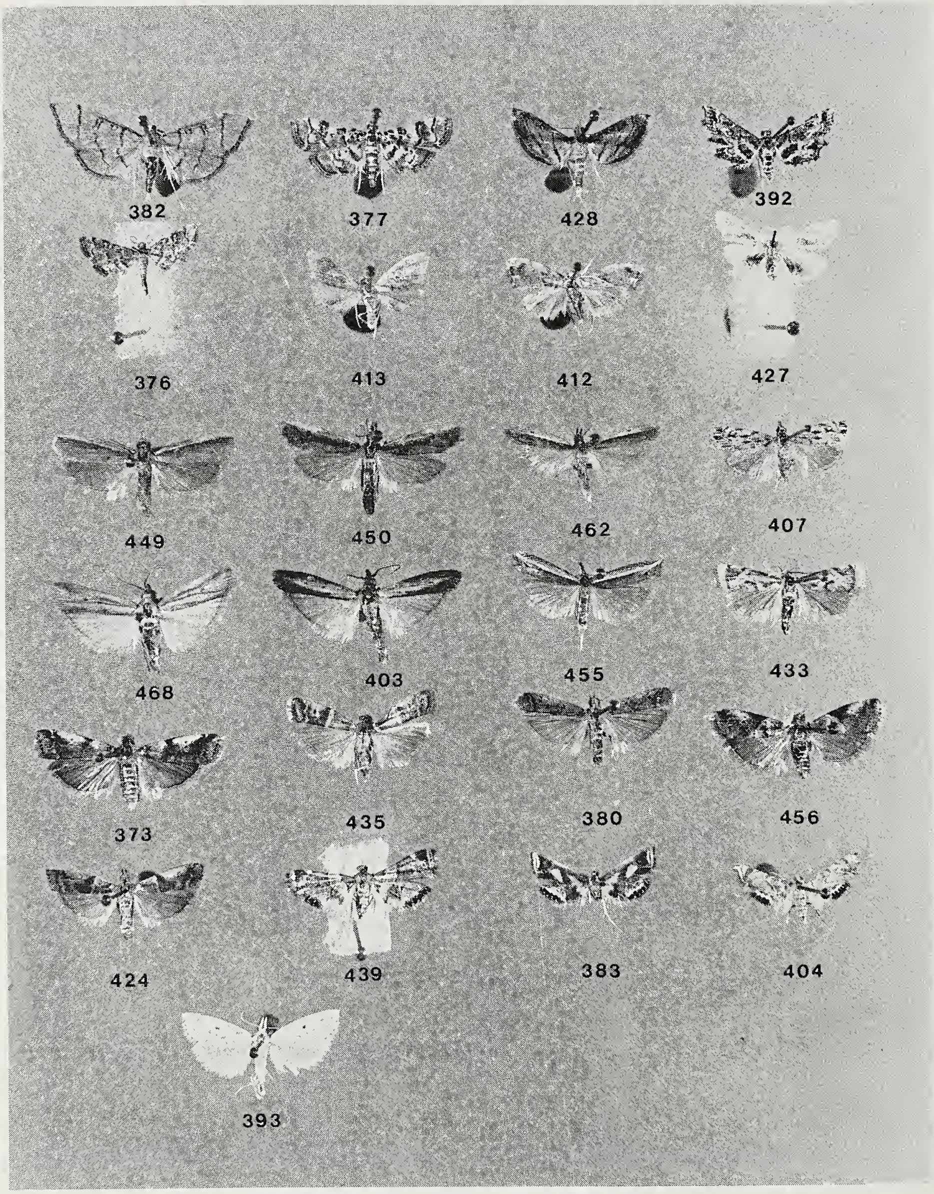
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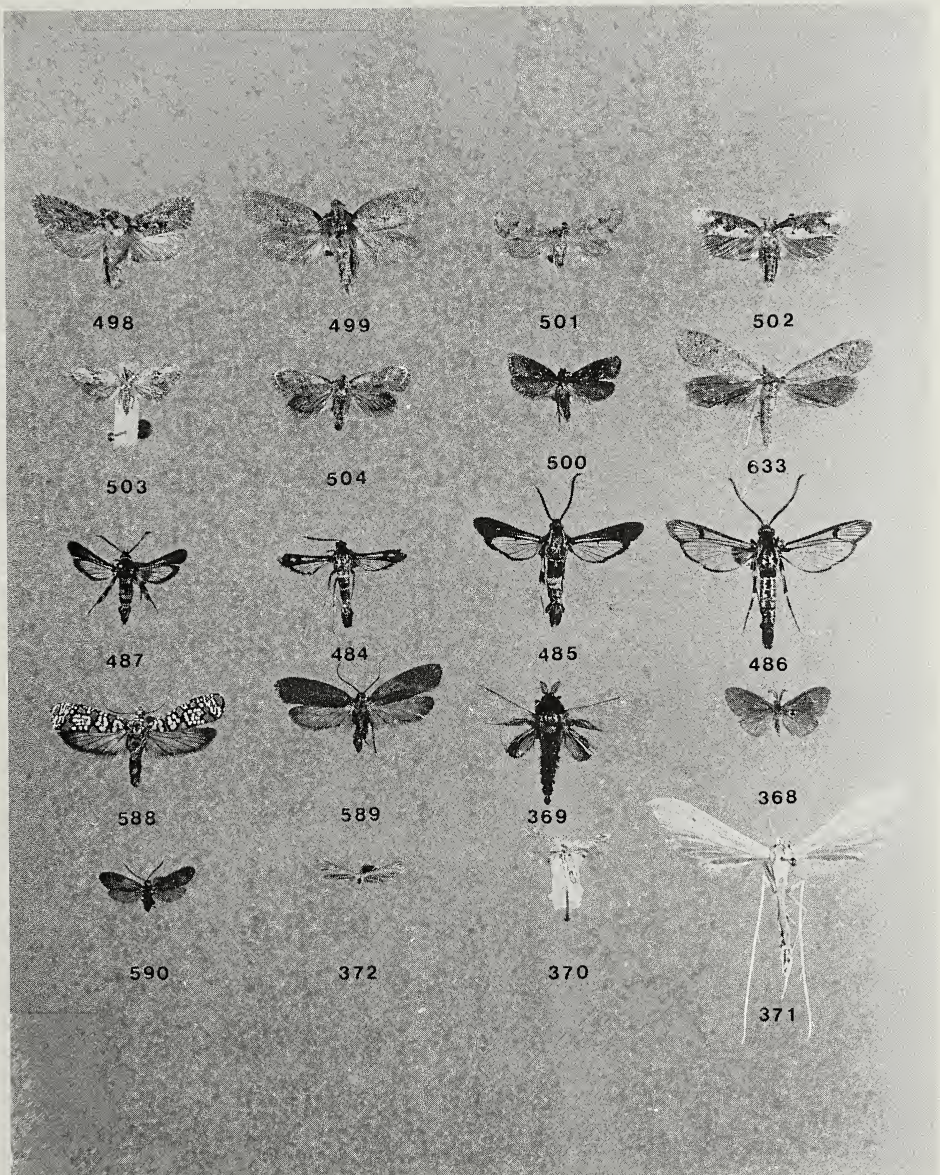
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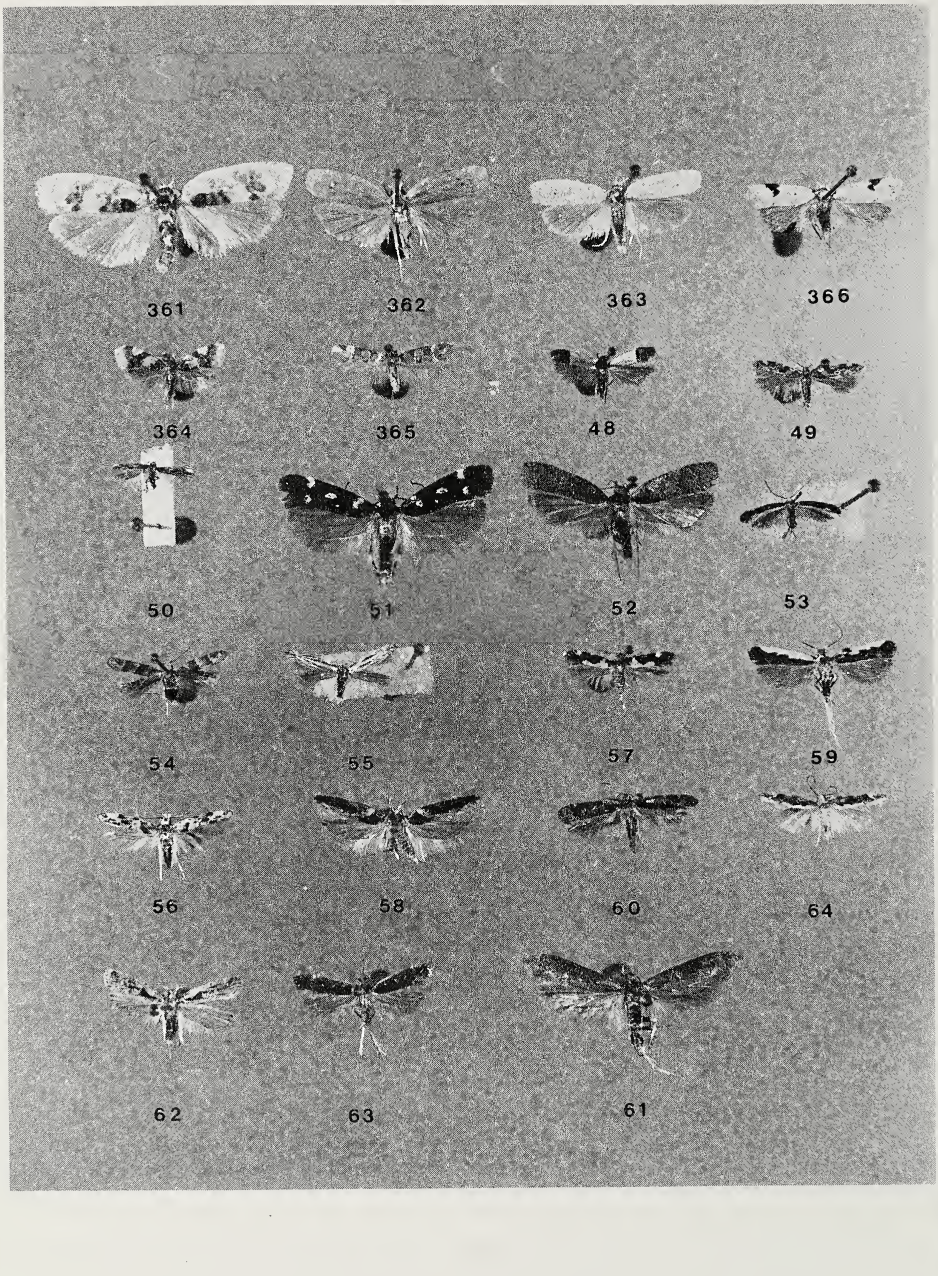
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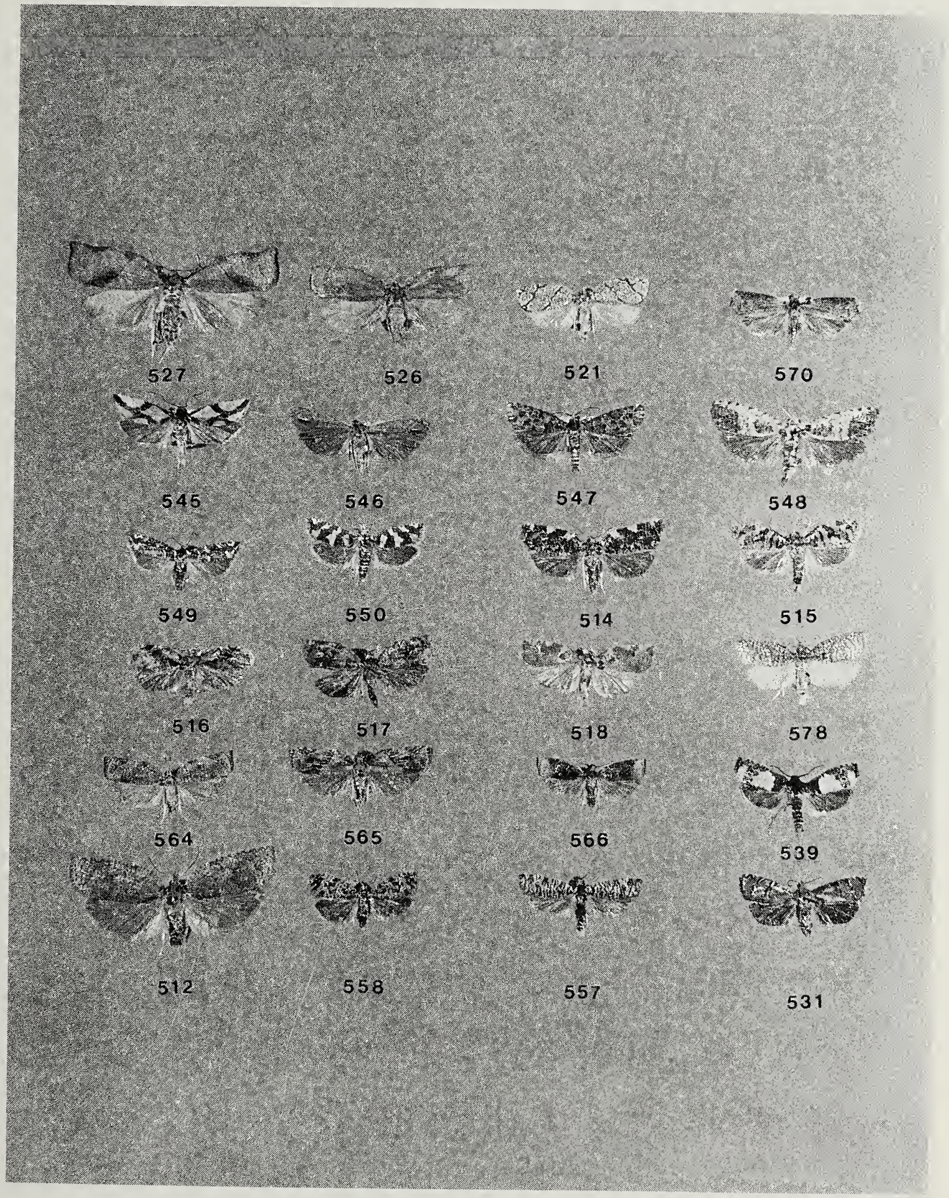
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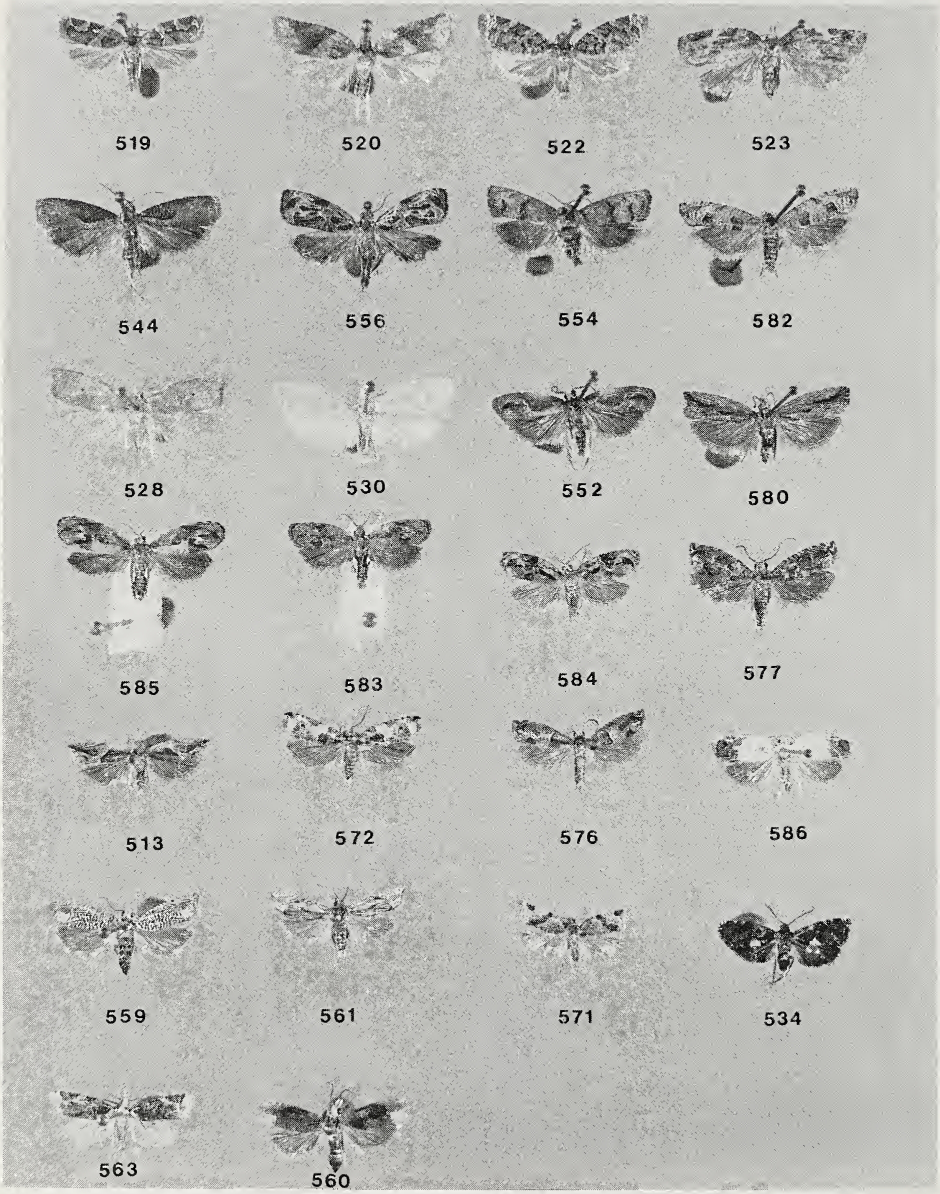
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New Records of Lepidoptera for New York and New Hampshire *(Nymphalidae, Noctuidae)*

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Abstract. Recent collecting in the Northeast has added the following Lepidoptera species to our regional lists: *Aglais urticae* (Linneaus) [Nymphalidae], *Syngrapha abstrusa* Eichlin & Cunningham, *Syngrapha montana* Packard, *Syngrapha microgamma* (Hübner), *Autographa rubida* Ottolengui, *Papestra quadrata* (Smith), *Anarta cordigera* (Thunberg), *Pachypolia atricornis* Grote, *Gabara subnivosella* Walker, *Xestia atrata* (Morrison), *Anomogyna rhaetica* (Staudinger), *Anomogyna fabulosa* Ferguson, *Apamea commoda* (Walker), *Oligia obtusa* (Smith), *Eutricopis nexilis* Morrison, *Bagisara rectilinea* (Grote), *Sympistis heliophila* (Paykull), *Sympistis funesta* (Paykull), *Macrochilo hypocritalis* Ferguson [all Noctuidae]. Dates, localities and life history notes are given and the species are illustrated. *Chamaedaphne calyculata* (L.) Moench [Ericaceae] is reported as a host for *Syngrapha microgamma*.

Introduction

Several summers spent rearing Lepidoptera in Albany's Pine Bush and in the Adirondack Mountains of New York, supplemented by several trips to Mount Washington in New Hampshire, has resulted in the discovery of several species that appear to represent new distribution records for the region. Some appear to be new to the continental United States or even North America. Detailed locality information is given in the legend below the plates. These records may not represent the first individuals ever collected at these localities, but are the first published report of which I am aware and represent noteworthy range extensions. Several papers appeared on the White Mountain Lepidoptera in the first issue of the journal Psyche. Of particular note is a paper by Morrison (1875) that lists Noctuidae. Forbes (1954) gives a recent synopsis of the Lepidoptera fauna for our region and makes many references to the higher elevations. The new records are as follows.

Nymphalidae

Aglais urticae (Linneaus). [Fig. 1]. A colleague, Charles Sheviak, discovered this butterfly flying on the grounds of the New York State Museum in downtown Albany, directed me to the spot, and I netted it after watching it frequent bare spots of ground where it would bask.

Emmons (1854) reported this as having been collected in the vicinity of Albany in 1853. However, no North American specimens were found in the New York State Museum's collection and Emmons' work was not well received. Emmons was a geologist and criticisms of his work included this comment by Schwarz (1892): "There are several instances on record where useless books have been printed at the public expense, but there has never been a more striking illustration of waste of money." In correspondence, Asa Fitch wrote, "Like his volume on Fruits, this on Insects, I think, must fall still born from the press" (Barnes, 1984). Possibly as a consequence of the lack of authority, catalogors have ignored Emmons report of *Aglais urticae*. Indeed, Emmons may well have meant to illustrate *Nymphalis milberti* inasmuch as no mention is made of that species' occurrence in New York. Also, specimens of *A. urticae* from Europe were apparently available to Emmons. All this notwithstanding, the present findings lends credence to the 1853 records.

The butterfly's occurrence, by any means, is not natural. Albany is an important port of commerce. The butterfly is univoltine at this latitude and the adult overwinters. It should be looked for very late and very early in the season to determine if it has become established. The example figured is clearly the nominate race and is found throughout western Europe, across Russia and Asia, and east to the Pacific coast of the Palearctic region.

Noctuidae

Syngrapha abstrusa Eichlin & Cunningham. [Fig. 2]. A distribution map is provided in the original description (1978). Its discovery in the Adirondacks was not unexpected.

Syngrapha montana Packard. [Fig. 3]. Described from Mt. Washington, I have taken a specimen at ultraviolet light at Lake Tear well below tree line on Mt. Marcy. In addition, I have taken a specimen at flowers in the daytime on Mt. Washington. It is decidedly rare in the East. Ferguson (1955) cites additional records.

Autographa rubida Ottolengui. [Fig. 4]. This boreal species was taken in the Adirondacks on *Apocynum* blossoms at night. Eichlin and Cunningham (1978) show a distribution dot for the Adirondacks, but I have been unable to locate the specimen.

Syngrapha microgamma (Hübner). [Fig. 5]. Ferguson (1955) has described the North American population as race *nearctica*. I swept two mature larvae (Fig. 20) from *Chamaedaphne calyculata* (L.) Moench [Ericaceae] on a bog near Raquette Lake in the Adirondacks. One was reared to adult and I have several light-trapped specimens from the same bog as well as from Bloomingdale bog in Franklin County, New York.

Papestra quadrata (Smith). [Fig. 6]. McCabe (1980) gives a distribution map of this species. One specimen was taken above tree line on Mt. Washington in New Hampshire at ultraviolet light.

Anarta cordigera (Thunberg). [Fig. 7]. This day-flying, bog-inhabiting species has been recorded from nearby Hawley bog in Massachusetts and is much more general to our north. I have it from three different bogs near the Browns Tract Ponds in the Adirondacks (all Hamilton County).

Pachypolia atricornis Grote. [Fig. 8]. This moth occurs later in the season than when most people collect. I have taken it in late September in the Adirondacks. I recently identified one for John Glaser which he had collected on Warrion Mt., Allegany Co., Maryland, on November 3rd, 1987, so it may prove to be much more widespread in the East than formerly recognized.

Gabara subnivosella Walker. [Fig. 9]. I have taken several specimens in Albany's Pine Bush. They represent a coastal form known as *bipuncta* (Morrison). According to Richards (1942) this form is most common in salt marshes, but also occurs in some inland marshes and he reported in from Long Island. I have it from dry, sandy barrens in Albany's Pine Bush.

Xestia atrata (Morrison). [Fig. 10]. Found just above tree line and in the krummholz on Whiteface Mt. It is known from Mt. Washington in New Hampshire and from numerous Canadian localities. Lafontaine, et al., (1987) give a distribution map. The example illustrated represents the nominate race.

Anomogyna rhaetica (Staudinger). [Fig. 11]. This species is the *sincera* mentioned by Forbes (1954) as being from Glens Falls. The Glens Falls locality seems suspect as this is a krummholz species and I have recorded it from Whiteface Mt. in the Adirondacks. The moth has also been associated with the name *Anomogyna homogena conditoides* Benjamin (see Ferguson, 1965).

Anomogyna fabulosa Ferguson. [Fig. 12]. This recently described species has been recorded from the White Mountains of New Hampshire and in Canada. I took it in the krummholz on Whiteface Mt. and also at Lake Tear on Mt. Marcy.

Apamea commoda (Walker). [Fig. 13]. Walker's type locality is not known for certain and Forbes (1954) suggests Trenton Falls, N.Y. Three specimens were taken in the krummholz on Whiteface Mt.

Oligia obtusa (Smith). [Fig. 14]. This moth may be utilizing roadside *Rumex*. It has been recorded from Albany's Pine Bush. I kept the solitary female specimen alive in the hopes of obtaining eggs (unsuccessfully) as a consequence the specimen figured has become very rubbed.

Eutricopis nexilis Morrison. [Fig. 15]. I took adults, which are diurnal, and (later in the season) larvae (Fig. 22) on the blossoms of *Antennaria canadensis* Greene in the Adirondacks. Hardwick (1970) describes the biology of the species.

Bagisara rectifascia (Grote). [Fig. 16]. This has been collected on Albany's Pine Bush and may be a new arrival. Increased use of ornamental Malvaceae may account for its recent occurrence.

Sympistis heliophila (Paykull) (=*melaleuca* (Thunberg)). [Fig. 17]. This species and the next occur above tree line and are day-flying and extremely difficult to catch. I collected a larvae (Fig. 21) of this species on *Vaccinium uliginosum* L., but it eventually died. A photograph of the larva was identified. Adults were also taken on Mt. Washington. They fly mid-morning on sunny days and can be taken when they bask on rocks.

Sympistis funesta (Paykull). [Fig. 18]. Douglas Ferguson [pers. comm.) has also recorded this moth from Mt. Washington. Its adult habits are similar to the former species.

Macrochilo hypocritalis Ferguson. [Fig. 19]. Members of this genus are found in wet places. The Black Creek, Albany Co., N.Y. locale has provided many swamp species including four other *Macrochilo* species.

Acknowledgements. I thank Charles Sheviak for calling my attention to the *Aglais* on the Museum's grounds. Kauri Mikkola, acting on my behalf, forwarded my photograph of the larva of *Sympistis heliophila* where it was kindly identified by E.O. Peltonen. All specimens were collected by the author. Christopher Supkis prepared the photographs. Douglas Wolfe of the Atmospheric Sciences Research Center extended every courtesy towards my collecting efforts on Whiteface Mt. Both James R. Jordan, Forest Supervisor, and, more recently, Gary W. Carr, District Ranger, of the White Mountain National Forest, granted permission for collecting moths on Mt. Washington. To all the above I am most grateful. Contribution number 572 of the New York State Science Service.

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Fig. 1.	*Aglais urticae*. Albany, Albany Co., N. Y., 19 October 1987, elev. 100 meters;
Fig. 2.	*Syngrapha abstrusa*. South Inlet, Raquette Lake, Hamilton County, N.Y., lat. 43.48.16 long. 74.36.30, 17 July 1977, elev. 555 meters;
Fig. 3.	*Syngrapha montana*, Lake Tear, Essex Co., N.Y., lat. 44.06.25 long. 73.56.05, 10 July 1980, elev 1310 meters;
Fig. 4.	*Autographa rubida*, 10 kilometers east of Indian Lake, Hamilton Co., N.Y., lat. 43.45.30 long. 74.10.14, 10 June 1977, 555 meters;
Fig. 5.	*Syngrapha microgamma*, 10 kilometers east of Indian Lake, Hamilton Co., N.Y., lat. 43.45.30 long. 74.10.14, 4 June 1977, 555 meters;
Fig. 6.	*Papestra quadrata*, Mt. Washington, Coos County, N.H., lat. 44.16.13 long. 71.18.02, 11 July 1985, elev. 1856 meters;
Fig. 7.	*Anarta cordigera*, Browns Tract Pond, Hamilton Co., N.Y., lat. 43.48.00 long. 74. 42. 17, 20 May 1980, elev. 555 meters;
Fig. 8.	*Pachypolia atricornis*, 10 kilometers east of Indian Lake, Hamilton Co., N.Y., lat. 43.45.30 long. 74.10.14, 30 September 1980, 555 meters;
Fig. 9.	*Gabara subnivosella*, Pine Bush, Albany Co., N.Y., lat. 42.42.19 long. 73.53.17, 9 July 1978, elev. 100 meters.

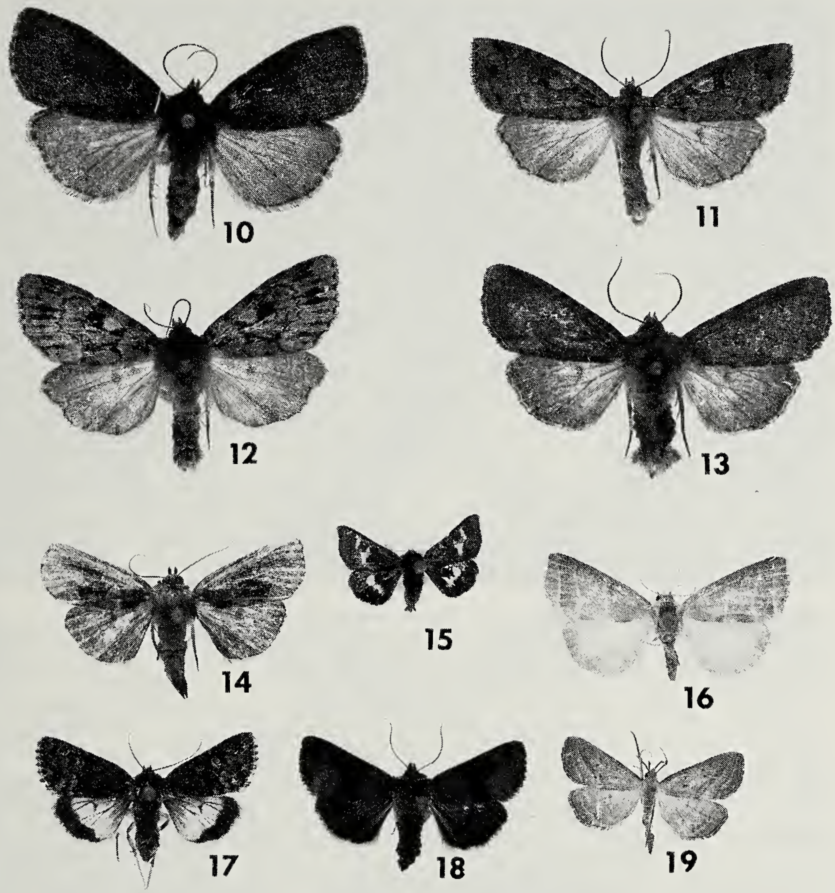

Fig. 10. *Xestia atrata*, Whiteface Mt., Essex Co., N.Y., lat. 44.22.58 long. 73.54.15, 6 July 1986, elev. 1065 meters;
Fig. 11. *Anomogyna rhaetica*, Whiteface Mt., Essex Co., N.Y., lat. 44.22.58 long. 73.54.15, 6 July 1986, elv. 1065 meters;
Fig. 12. *Anomogyna fabulosa*, Whiteface Mt., Essex Co., N.Y., lat. 44.22.58 long. 73.54.15, 6 July 1986, elev. 1065 meters;
Fig. 13. *Apamea commoda*, Whiteface Mt., Essex Co., N.Y., lat. 44.22.58 long. 73.54.15, 6 July 1986, elev. 1065 meters;
Fig. 14. *Oligia obtusa*, Pine Bush, Albany Co., N.Y., lat. 42.42.19 long. 73.53.17, 24 July 1987, elev. 100 meters;
Fig. 15. *Eutricopis nexilis*, 6 miles east of Indian Lake, Hamilton Co., N.Y., lat. 43.45.30 long. 74.10.14, 29 May 1980, 555 meters;
Fig. 16. *Bagisara rectilinea*, Pine Bush, Albany Co., N.Y., lat. 42.42.19 long. 73.53.17, 17 July 1986, elev. 100 meters;
Fig. 17. *Symistis heliophila*, Mt. Washington, Coos County, N.H., lat. 44.16.13 long 71.18.02, 17 July 1984, elev. 1856 meters;
Fig. 18. *Sympistis funesta*, Mt. Washington, Coos County, N.H., lat. 44.16.13 long 71.18.02, 17 July 1984, elev. 1856 meters;
Fig. 19. *Macrochilo hypocritalis*, Black Creek, Albany Co., N.Y., lat. 42.39.53 long. 74.58.01, 3 July 1984, elev. 100 meters.

Fig. 20. *Syngrapha microgamma*, South Inlet, Raquette Lake, Hamilton County, New York, lat. 43.48.16 long. 74.36.30, 17 May 1980, elev. 555 meters;

Fig. 21. *Sympistis heliophila*, Mt. Washington, Alpine Gardens, Coos County, New Hampshire, lat. 44.16.13 long. 71.18.02, 15 July 1981, elev. 1856 meters.

Fig. 22. *Eutricopis nexilis*, 10 kilometers east of Indian Lake, Hamilton County, New York, 12 June 1980, lat. 43.45.30 long. 74.10.14, elev. 555 meters.

Suppression of the black pigment in female hybrids of *Papilio glaucus* and *P. multicaudatus*: further evidence of the value of ecdysone in breaking pupal diapause.

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Abstract. Using injections of ecdysone it was possible to break indefinite pupal diapause in female hybrids between a black *Papilio g. glaucus* female and a male *P. multicaudatus*. The insects demonstrate well-marked suppression of the black *glaucus* pigment.

In previous papers (Clarke, Sheppard and Willig, 1972; Clarke and Willig, 1977 and West and Clarke, 1988) we showed that the black pigment of *Papilio glaucus* females could be suppressed in varying degrees in hybrids using males of *Papilio rutulus*, *Papilio glaucus canadensis* and *Papilio eurymedon*, and probably also with *Papilio multicaudatus*. However, there was some doubt about the last (see West and Clarke, 1988, page 197) as the two yellow females recorded in a back-cross brood (female black *glaucus* × male F1 *glaucus* × *multicaudatus*) were lost from our collection. The present paper remedies this carelessness.

Materials and Methods

On 11. VII. 1987, using the hand-pairing technique (Clarke, 1952) we crossed a black female *P. glaucus* (ex 1986 stock obtained from Pasadena, Maryland, U.S.A.) with a *P. multicaudatus* male (obtained from pupae sent by David V. McCorkle and originating from Klickitat Co. Washington). The caterpillars (brood 19052) were fed on *Liriodendron*, and produced 13 male butterflies by 1. IX. 1987. A further two male pupae overwintered but only produced deformed insects in April, 1988, i.e. 15 males in all.

We scored 13 of the pupae as being female but none of them eclosed.

Seven were therefore given cold/hot shock treatment (see footnote) some by Mr. Karl Bailey and some by Mr. George Beccaloni, but this was unsuccessful and by 30. III. 1989 we only had six (untreated) pupae left alive. We therefore decided to try the use of ecdysone preparations and one of us (HHR) carried out the injections. The six pupae were divided into two groups of three, one batch being injected with ecdysone and the other with 20-hydroxyecdysone, but the latter was unsuccessful, all the pupae dying, possibly because the action of the hormone was too rapid. To the other three pupae six ecdysone injections, each of 170 ng, were given (as in Clarke and Willig, 1977) on 3, 6, 8, 10, 12 and 14, IV. 1989.

Results

Three females emerged between 29. IV. 1989 and 2. V. 1989 and are shown in Figure 1. It will be seen that only one (No. 1) grew fully, but this is clearly primarily a yellow insect though with some "sooty" features. (Black females normally always produce black daughters and yellow females yellow ones.) The second hybrid (No. 2) failed to grow, but it seems likely that had it done so it would have resembled No. 1. No. 3 is more problematical — it too did not grow and is a good deal blacker, but there is some yellow pigment in the hindwing. Suppression of black therefore is probably variable.

We can therefore safely conclude that the male *multicaudatus* does carry a suppressor of black, probably autosomally controlled (see West and Clarke, 1988) though the expression is variable.

Discussion

It is easy to surmise that the presence of a suppressor would protect the insect in areas where the model *Battus philenor* does not fly and a black mutant would then be disadvantageous. However from an evolutionary point of view these "anticipatory" theories are troublesome, the rather lame explanation being that the "waiting" gene must have been doing "something else". The same problem occurs in Man with certain drugs, for example isoniazid — where there is a precise dimorphism for the rates at which the drug is metabolised. However the gene controlling this must have been present millions of years before isoniazid was synthesised.

Acknowledgements. We thank Mr. Karl Bailey and Mr. George Beccaloni for carrying out the temperature experiments and are grateful to Professor B. Surholt and Herr H. Brockhoff for useful discussions. We are indebted to the Nuffield Foundation for its generous support.

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Fig. 1. Fl hybrid females of the cross ♀ black *P. glaucus* X ♂ *P. multicaudatus* (see text).

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Footnote

Details of Mr. Karl Bailey's cold/hot shock therapy.

On 17.XI. 1987 the hybrid pupae were refrigerated at −4.5°C ± .5°C and left for 8 weeks. They were then transferred to an incubator at 26°C in the hope that the diapause would be broken. This did not occur and the pupae died.

Details of Mr. George Beccaloni's cold/hot shock therapy.

Pupae received on 8. II. 1989 and placed in a refrigerator at 0°C where they were kept for three months. They were removed on 7. V. 1989 and subsequently kept at room temperature. They did not emerge and were given our standard ecdysone treatment beginning on 9. VI. 1989. They were then kept at room temperature but all died and no insects had formed up inside them.

Journal of Research on the Lepidoptera 28(1-2):88-96, 1989(90)

Studies on Spatial Distribution in the Teak Carpenterworm *Cossus cadambae* Moore (Lepidoptera, Cossidae)*

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Abstract. *Cossus cadambae* Moore (Lepidoptera, Cossidae) is a relatively new insect pest of teak in India and it has recently assumed major pest status in several plantations in Kerala, Tamil Nadu and Karnataka States. Caterpillars of this insect characteristically bore in the wood of standing trees leading to deterioration of timber. *C. cadambae* has annual generations with an exceptionally prolonged larval stage. At Palappilly, Kerala, where the study was carried out, the generations were continuous and overlapping. The progression of infestation intensity among the trees was studied here. The intensity of attack was studied by scoring the affected trees visually into the following score classes viz., 0 = healthy tree; 1 = low level infestation with a few scattered borer holes; 2 = medium level of infestation with borer holes confined to small groups; 3 = heavy infestation with numerous borer holes in large patches all over the stem and 4 = tree dead as a result of heavy infestation. The results show that during the initial phase of infestation a considerable number of trees in a plantation get affected. The intensity of infestation during this stage remains at a low level (score 1) and usually goes unnoticed since the feeding scars are not often easily detectable. During the subsequent phase of infestation there is a tendency for the already affected trees to get reinfested, besides fresh attack to the unaffected trees in the plantations. As a result there is slow transfer of trees of low intensity score to high intensity classes (score 2, 3, 4) and the affected trees generally occur in distinct patches. As the infestation progresses, further recruitment of attacked trees to higher scores of infestation intensity take place. This phase is characterised by large-scale mortality of the heavily affected trees (score 4). As more and more healthy trees get affected, the infestation becomes more or less uniformly distributed throughout the plantation obliterating the original patchy infestation.

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[1]Entomology Division, [2]Management Division

Introduction

Teak (*Tectona grandis* Lin.f.) is an important forest tree species raised in extensive plantations in several parts of India, notably in Madhya Pradesh, Andhra Pradesh, Karnataka, Tamil Nadu and Kerala States. In Kerala alone, there are over 60,000 ha. of area planted with this species.

About 140 species of insects are known to attack this tree in the Indian sub region (Nair & Kumar, 1986) although only a few have been reported to cause major damage in plantations. This includes 2 species of follage feeders viz., *Hyblaea puera* Cram. (Hyblaeidae) and *Eutectona machaeralis* Wlk. (Pyraustidae) and a sapling borer *Sahyadrassus malabaricus* Moore (Hepialidae). Recently, outbreaks of a wood boring insect viz., *Cossus cadambae* (Cossidae) have been noticed in several teak plantations in Kerala, Tamil Nadu and Karnataka States in India (Mathew, 1988).

C. cadambae mostly attacks mature teak trees. The caterpillars of this insect initially get established in the bark surrounding a wound caused by mechanical injury or in the axillary region of branches (Fig. 1). Subsequently they bore into the sapwood and then into the heartwood. The larval stage lasts for about 8 months and the fully mature larvae measure about 5 cm in size. One caterpillar makes only a single borer hole although heavy infestation over several years can lead to the formation of numerous holes on the wood.

In Kerala, infestation by *C. cadambae* was observed mostly in plantations adjacent to human habitations. Trees growing in such areas were frequently subjected to mechanical damages such as lopping of branches, plucking of leaves etc. Usually, trees along the borders or those standing along the sides of forest tracks were repeatedly subjected to this type of damage. Such trees were often found to be heavily attacked while those occurring in the interior or inaccessable areas were not affected. Mechanical injury leads to the formation of callus growth over wounds or profuse growth of coppices which offer conditions favourable for the establishment of this insect. Beeson (1941) also considered mechanical damage as a factor promoting cossid infestation.

Presently there is no information available on the establishment pattern of this insect in plantations over space and time. Such information is needed for development suitable management strategies and therefore an attempt was made to study this aspect in selected plantations of varying intensity of infestation.

Materials and Methods

Data for this study were collected from three borer-infested teak plantations in Kerala, which were selected to represent three distinct phases in the establishment of this insect. These phases include (i) an initial stage when the

Fig. 1 Trunk of teak showing damage by *C. cadambae*

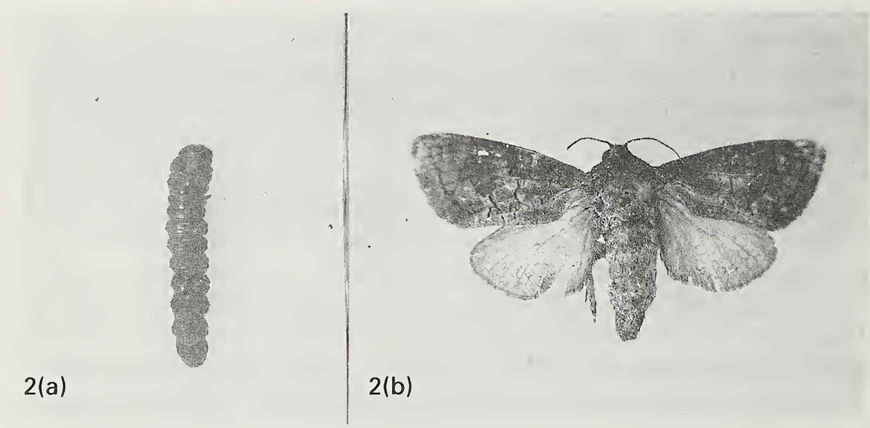

Fig. 2(a) Larva of *C. cadambae*; 2(b) moth

affected trees show only low level infestation, with a few borer holes on the trunk, (ii) an advanced stage of infestation characterised by the formation of several holes on the stem and (iii) a later stage when the damage intensity has substantially increased resulting in many holes on the wood, rendering it unfit for any commercial use. Plantations having the above situations were selected at Parambikulam, Thattakad and Palappilly respectively, based on a sampling survey taking into account the number of affected trees as well as their damage

intensity (Table 2). The intensity of attack was rated by scoring the affected trees visually as given below.

0 = healthy tree
1 = low level of infestation ie., with few scattered borer holes
2 = medium level of infestation with several borer holes usually confined to samll groups
3 = heavy infestation with numerous borer holes in large patches all over the stem
4 = tree dead as a result of heavy infestation

In each of the plantations selected for study, a series of rectangular plots (Table 1) of size 20 m × 8 m were taken linearly extending from one boundary to the other. Each plot contained 34 trees depending on the terrian as well as the extent of disturbance due to various factors like illicit felling, windfall etc. The number of healthy and affected trees as well as the intensity of attack on each of the affected trees was recorded. A negative binomial distribution was fitted to the data on the number of trees affected per plot, in the Parambikulam and Thattaked plantations. Similarly a binomial distribution was fitted to the data on the number of trees affected in the Palappilly plantations. The probability density function of the negative binomial is

$$P(x) = \left(\frac{k + x - 1}{x}\right) \left(\frac{\mu}{k + m}\right)^x \left(1 + \frac{\mu}{k}\right)^{-k}$$

where P(x) is the probability of x individuals of a given attribute in the sampling unit
μ is the location parameter,
k is the dispersion parameter
and that of the binomial is

$$P(x) = \left(\frac{n}{x}\right)^{p^x q^{n-x}}$$

where P is the proportion of the population that shows the attribute q is (l − p) and n is the maximum number of individuals in the sampling unit.

The parameters in both the cases were estimated through the method of maximum likelihood. The methods given in Bliss and Fisher (1953) were followed in fitting the negative binomial distribution.

Results and Discussion

Data on the infestation status at the three localities studied herein are given in Table 1. The percentage of affected trees was comparatively low at Parambikulam (19.08%) and Thattaked (17.64%) as compared to that of Palappilly (83.84%). Although the percentage of affected trees in the first two localities were more or less the same, the intensity of infestation in each of these plots was found to vary.

At Parambikulam all the affected trees belonged to a single intensity score class (score 1) while at Thattakad the affected trees belonged to all the four intensity classes. The data for the third locality Palappilly, showed a marked increase in the percentage of affected trees (83.84%).

Table 1. Basic features of the data gathered from 3 localities

Locality	Number of plots	Total No. of trees	% of trees affected under the various score classes 0	1	2	3	4
Parambikulam	90	414	80.92	19.08	–	–	–
Thattakad	90	323	82.35	5.57	4.02	5.57	2.48
Palappilly	73	167	16.16	6.59	11.98	26.35	38.92

Table 2. Estimates of the parameters for the fitted distributions and goodness of fit

Locality	Variable	Binomial distribution p	χ^2	Negative binomial distribution μ	k	χ^2
Parambikulam	V_1	0.76	3.80 (ns)			
Thattakad	V_1	0.72	26.18 (**)			
Palappilly	V_1	0.46	7.79 (ns)			
Parambikulam	V_2			0.87	11.15	6.34 (ns)
Thattakad	V_2			0.62	2.62	5.77 (ns)
Palappilly	V_2	0.39	5.85 (ns)			

V_1 = Number of trees present per plot
V_2 = Number of trees affected per plot
ns = non significant
** = significant at 1%

When the relative numbers of affected trees belonging to the various score classes at Thattakad and Palappilly were examined, we found that there was a transformation of the affected trees from the low intensity score to the higher scores with a certain extent of mortality of trees. That is, at Thattakad, out of 17.64% affected trees, only 5.57% belonged to score 1 and the remaining trees belonged to the other score classes (Table 1). Similarly at Palappilly there was a tendency for increase in the number of trees belonging to the high score classes (score 2 = 11.98%, score 3 = 26.35%). The site was also characterised by a high rate of tree mortality (score 4 = 38.92%) and thus only a small percentage of trees belonged to score 1 (score 1 = 6.59%).

The infestations at each of the above localities were very characteristic and illustrated the various phases in the establishment of this insect. The situation observed for Parambikulam represents the initial phase, when the trees show only minimum damage with few borer holes on the trunk. The situation at Thattakad represents the second phase, when the already affected trees were subjected to reinfestation in the subsequent years when the damage became more pronounced often leading to mortality of some trees. In the third phase as represented at

Fig.3a Parambikulam

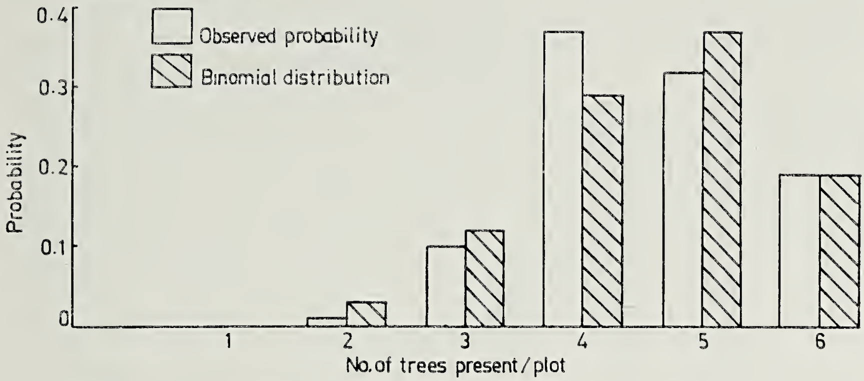

Fig.4a Thattakkad

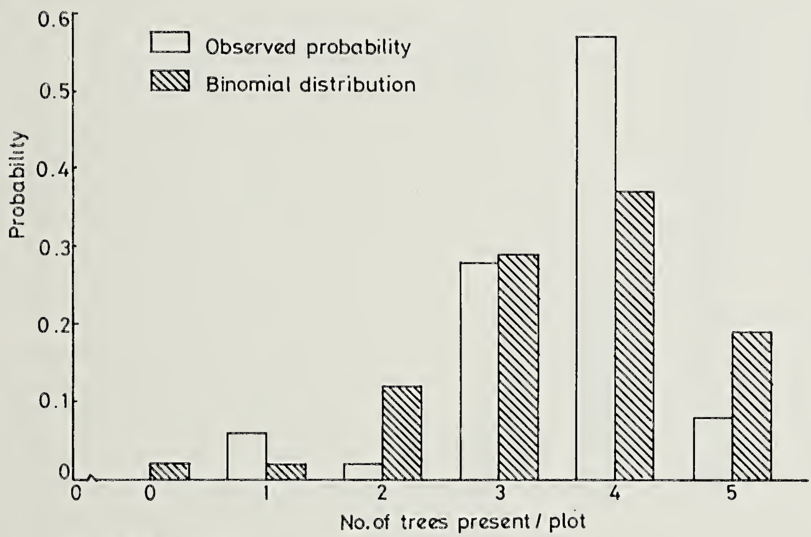

Fig. 5a Palappilly

Fig. 3a, 4a, 5a Distribution of number of trees present/plot in Parambikulam, Thattakad and Palappilly.

Fig. 3b Parambikulam

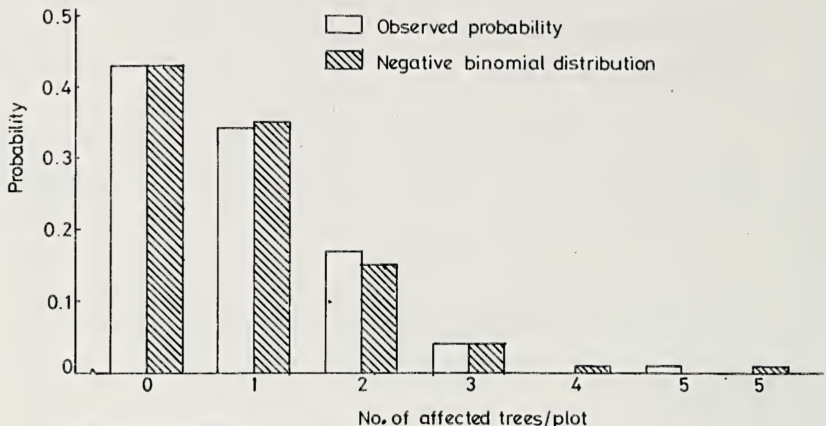

Fig. 4 b.Thattakad

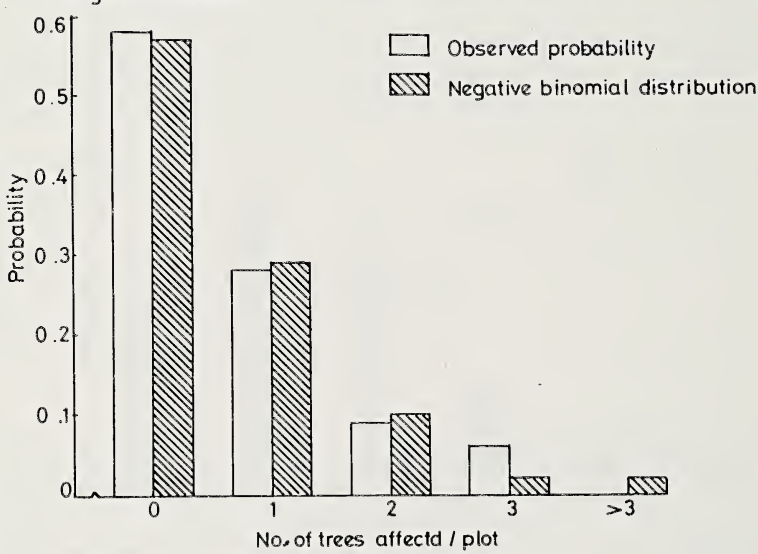

Fig. 5 b Palappilly

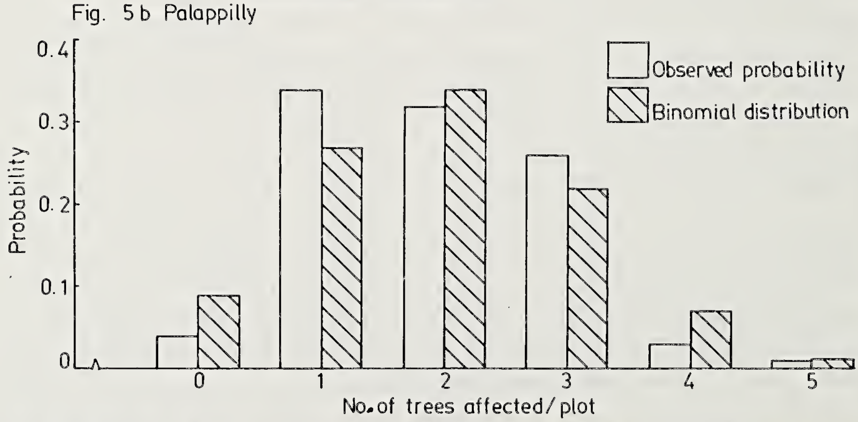

Fig. 3b, 4b, 5b Distribution of number of trees affected/plot in Parambikulam, Thattakad and Palappilly.

Palappilly, there was a marked increase in the number of affected trees belonging to higher intensity scores besides fresh attack on the unaffected trees over years resulting in extensive riddling of the timber and subsequent large scale tree mortality.

We studied the distribution of two variables, number of trees present per plot and the number of trees affected per plot, in each of the three localities. The test of independence between the two variables in different plots showed them to be dependent in the case of Palappilly ($\chi^2 = 144.73$) and independent in the cases of Thattakad ($\chi^2 = 5.81$) and Parambikulam ($\chi^2 = 11.86$). Therefore it was necessary to study the distribution of variables in the three localities separately. The estimates of the parameters in the fitted distributions are given in Table 2. It indicates that the variable, the number of trees affected per plot, follows negative binomial distribution in the cases of Parambikulam and Thattakad and binomial distribution in the case of Palappilly (Fig. 3b, 4b, 5b). That is, the affected trees occur in definite patches or clusters in Parambikulam and Thattakad, while at Palappilly the affected trees were uniformly distributed. The reason for the uniform distribution of affected trees at Palappilly might be due to the patches of affected trees becoming confluent with the progression in the infestation level over a period of time. The distribution of the number of trees present per plot, was found to be binomial in the case of Parambikulam and Palappilly (Fig. 3a, 5a). However, in the case of Thattakad it was not so (Fig. 4a) probably due to irregularities in the actual frequencies of trees per plot.

The time taken for transformation from one phase of infestation to the other could not be arrived at but it seems that this change is a slow one perhaps requiring several years due to the biology of this insect.

The study has shed some light on the distribution pattern of *C. cadambae* in teak plantations in Kerala under varying levels of infestation status. During the initial phase of attack, the infestation usually goes unnoticed since the feeding scars are usually not very prominent. At this stage a considerable number of trees get attacked. The second phase is characterised by further deterioration of the already affected trees due to reinfestation in the subsequent years leading to slow mortality of trees and by a slow spread of attack to the healthy trees in plantations. During these two phases the affected trees are usually confined to distinct patches. *C. cadambae* being highly mobile organisms can fly to the other parts of the plantation or even to other plantations in the vicinity, resulting in the spread of attack. During the last phase the infestation spreads at a faster pace leading to a high mortality of affected trees and a more or less uniform distribution of attack throughout the plantation.

Due to the behavioural characteristics of this insect, specialised pest management strategies need to be developed for its control in plantations. Since its attack is more clustered in the initial phase, manage-

ment operations need be confined to the affected patches only, rendering control operations more economical.

Acknowledgement. We are extremely grateful to Dr. C.T.S. Nair, Director, and Dr. K.S.S. Nair, Scientist in Charge, for their keen interest in this study. We thank Mr. Unnithan (Professor, Department of Statistics, Kerala Agricultural University, Vellanikkara) for useful suggestions and discussions during the course of this study and Dr. Paul D. Syme, Forest Insect and Disease Survey Unit, Great Lakes Forestry Centre, Ontario, Canada for critically reviewing this paper. Thanks are also due to Mr. E.P.S. Nair for neatly typing out the manuscript.

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A New Species of *Argyrotaenia* from Arizona (Lepidoptera: Tortricidae)

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Abstract. A new species of *Argyrotaenia* is described, figured and compared with *A. cockerellana* (Kearfott) from which it differs by the much darker forewing and longer aedeagus.

Mr. Ronald W. Wielgus has been studing and contributing to the knowledge of the lepidoptera of Arizona for many years. Among his recent discoveries, near his home, is a species of *Argyrotaenia* for which he needs a name, and which is described below. In addition to the specimens submitted by Mr. Wielgus, there is a series from Texas, which came to the National Collection in the gift of the late André Blanchard. Dr. John G. Franclemont of Cornell University and Dr. Ronald W. Hodges, U. S. Department of Agriculture, have given a series, also from Arizona, which is listed with the paratypes.

Argyrotaenia wielgusi, Clarke, new species (Figure 1)

Alar expanse 24–28 mm.

Labial palpus russet; third segment brown. Antenna russet. Head, thorax, and forewing ground color vinaceous-cinnamon; on basal half of costa four short brown bars and on apical half of costa four brown spots; on dorsal edge similarly colored but somewhat suffused markings; around termen four or five brown spots; from base to termen, following fold, a slender, dark brown line, broken about middle and overlain in part by dark brown blotches; from near base to near termen of forewing a series of irregular dark brown markings; near base of fold a small white mark; on costal edge of cell two conspicuous, white marks, the outer one split by a slender, transverse dark brown line; cilia vinaceous-cinnamon. Hindwing whitish, suffused grayish to pale gray, the veins clearly outlined darker gray; cilia sordid white, suffused grayish with a gray subbasal line. Foreleg tibia white on inner surface, vinaceous-cinnamon on outer surface; tarsal segments brown narrowly annulated buff distally; midleg similar; hindleg buff; tarsal segments lightly suffused grayish. Abdomen gray with some buff scales ventrally.

Male genitalia slides No. 26358, 26366, 26683, 26684. Harpe broad; costal half cupshaped, cucullus bluntly pointed; sacculus thickened and produced ventrally. Gnathos a long, slender, slightly curved process. Uncus stout, curved, slightly dilated distally. Vinculum a narrow

semicircle. Tegumen strongly sclerotized, longer than broad. Anellus triangular, deeply cleft posteriorly. Aedeagus longer than tegumen, slender, strongly curved; extension of the phallobase unusually developed.

Female genitalia slides No. 26359, 26388, 26389. Ostium very broad, funnelshape. Antrum narrow, strongly sclerotized. Inception of ductus seminalis from right side at junction of antrum and membranous portion of ductus bursae. Ductus bursae membranous. Bursa copulatrix membranous with little or no ornamentation. Signum a long, slender, hook.

A. wielgusi is very closely related to *A. cockerellana* (Kearfott), but is a much larger and darker species. *A. wielgusi* measures 24–28 mm., and the ground color of the forewing is vinaceous-cinnamon; *cockerellana* measures 14–22 mm., and the forewing ground color is light cinnamon-buff. The length of the aedeagus of *cockerellana* is about two-thirds the length of that of *wielgusi* and is not so strongly curved.

It gives me great pleasure to name this handsome moth for Mr. Wielgus in recognition of the many contributions to the knowledge of the lepidoptera of Arizona which he has made.

I thank Mr. Victor Kranz, Smithsonian staff, for the photographs of the moth wings and genitalia. Also, I am indebted to Mrs. Nancy L. McIntyre for typing the manuscript.

Holotype: United States National Museum of Natural History.

Type locality: Arizona, Cochise Co., Huachuca Mts., Pueblo del Sol.

Distribution: Arizona and Texas.

Food plant: Unknown.

Described from the ♀ holotype from Arizona: Cochise Co., Huachuca Mts., Pueblo del Sol (6.XI.1986, R. S. Wielgus), one ♀ paratype with same data except 5.XI.1985; one ♂ paratype, Cochise Co., Huachuca Mts., Ash Canon (15.XI.1985, Noel McFarland [found in water]); one ♂ paratype, Cochise Co., 5 mi. W. Portal, 5400', 17.X.1964, V. Roth; 3♂♂, 5♀♀ paratypes, Santa Cruz Co., Santa Rita Mts., Madera Canon, 4880', 22.X. to 7.XI.1959, J. G. Franclemont; 4♀♀ paratypes, same locality, 25–28.X.1959, R. W. Hodges. Texas: 7♂♂ paratypes, Davis Mts., Mt. Locke, 6700', 21.X.1973; 2 ♂♂ paratypes, Jeff Davis Co., Fort Davis, 23.X.1973, all A. and E. Blanchard.

There are two ♂♂ specimens from Montana, considerably smaller (20 mm.) than the Arizona and Texas specimens, that are not included in the type series, but the genitalia of which are indistinguishable. The Arizona specimens have a more violaceous tinge to the ground color, but otherwise are inseparable.

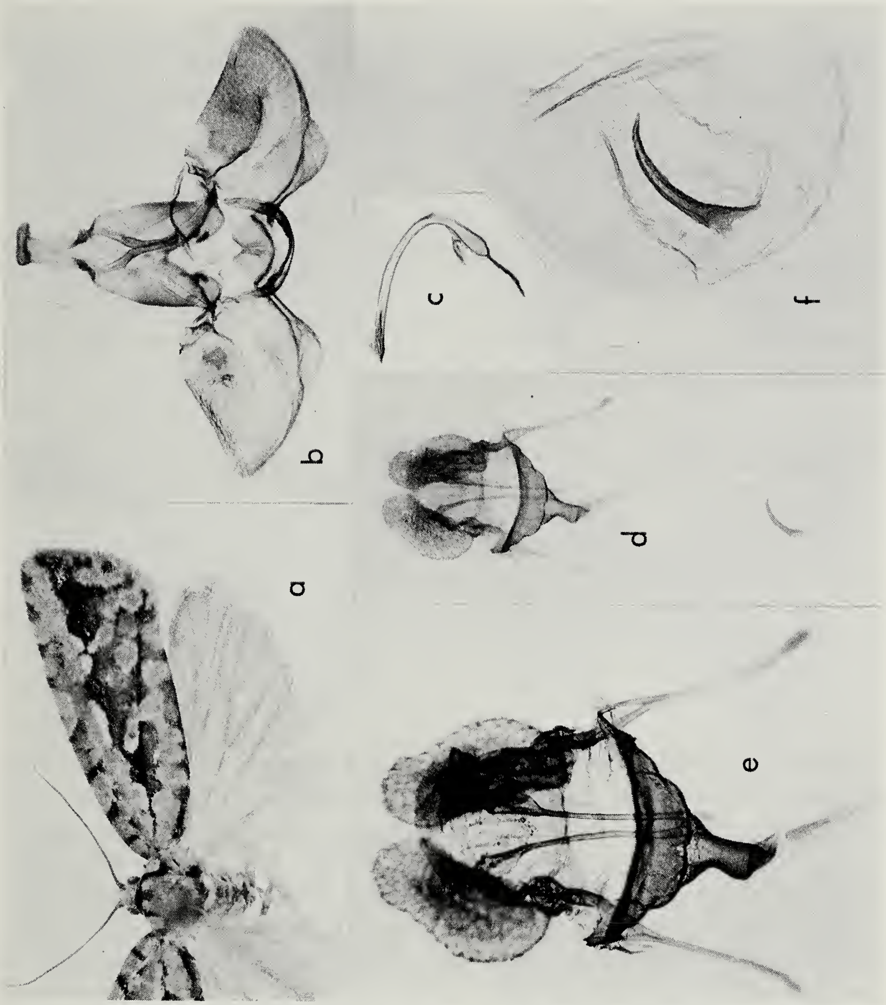

Fig. 1. a, right wings; b, ventral view of male genitalia with aedeagus removed; c, aedeagus; d, ventral view of female genitalia; e, enlarged view of papillae anales and ostium; f, enlarged bursa coplatrix and signum.

Journal of Research on the Lepidoptera 28(1-2):100-104, 1989(90)

A new subspecies of *Satyrium auretorum* (Lycaenidae) from the Santa Monica mountains of southern California

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Abstract. A new subspecies of hairstreak butterfly, *Satyrium auretorum fumosum*, is named to designate the differentiated endemic populations of the species that are restricted to the western end of the Santa Monica mountains in California.

Satyrium auretorum (Boisduval) is a widespread, but local, hairstreak species found throughout the foothills and lower mountain slopes of much of California. The nominotypical subspecies was described from a single male (Boisduval 1852), probably taken in the Feather River drainage in the northern Sierra Nevada foothills. For many years the species was considered a great rarity and even Comstock (1927) was unable to illustrate it in color due to the lack of specimens. Since then, however, collectors have taken it in numerous locations across the coast ranges and the Sierra Nevada foothills.

In 1881 Henry Edwards described a southern California subspecies, *spadix* (type locality, Tehachapi pass, California), which he characterized by a lighter ventral surface and more extensively developed fulvous scaling on the dorsal surface of females. This subspecies has subsequently been more frequently collected than the nominotypical one, a function of the greater concentration of collectors near its habitat. From all available information, the species is restricted to scrub oak chaparral and is wholly found within the California floral province.

In 1973 Emmel and Emmel made brief reference to an undescribed subspecies of *S. auretorum*, from the Santa Monica mountains of southern California, which they characterized by a phenotype darker than known from any other population. We now describe this distinct segregate as follows:

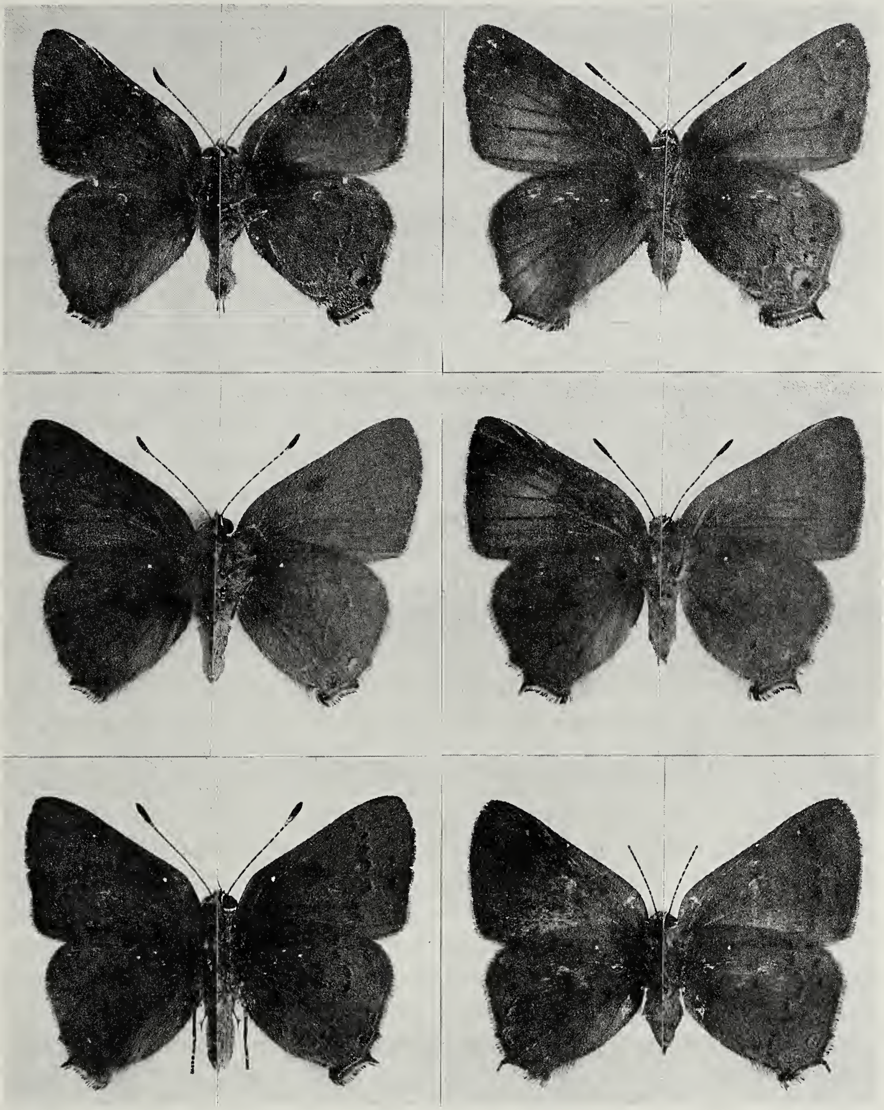

Fig. 1. The subspecies of *Satyrium auretorum*. Left half of each figure dorsal, right half of each figure ventral, surface. Left column males, right column females. Top row, *S. auretorum auretorum*, male, 4 mi. N. Camptonville, Sierra Co. CA. 29 June 1964; female, Capell creek, Napa Co., CA. 3 June 1966. Middle row *S. auretorum spadix*. NE slope San Gabriel Mts., Los Angeles Co., CA. male 6 June 1974; female 8 June 1974. *S. auretorum fumosum*, male, (holotype) Malibu Lake, Los Angeles Co., CA. 6 June 1948; female (allotype) same locality 16 June 1948.

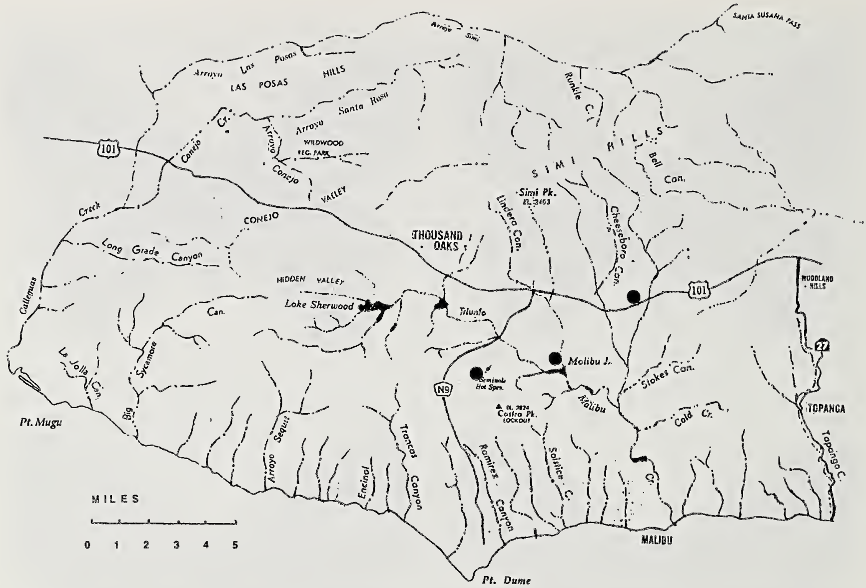

Fig. 2. Distribution map of *Satyrium auretorum fumosum* in the western section of the Santa Monica mountains. The entire known distribution of the subspecies is shown.

Satyrium auretorum fumosum Emmel and Mattoni **new subspecies**

MALE. Forewing length 12.5–13.5 mm, mean 13.1 mm (N=13).

Dorsal Surface. Forewing: Ground color dark brownish gray. Outer margin with a thin dark brown border, diffused basad into ground color. Fringe pale tannish gray. Androconial scales pale gray, standing out in greater contrast against the ground color than in either *auretorum* or *spadix*. Hindwing: Ground color, outer margin and fringe as in forewing. Anal area pale tannish gray. Tail black with white scaling at tip.

Ventral Surface. Forewing: Ground color dull brown, darker than the fulvous brown seen in nominotypical *auretorum* or *spadix*. Pale gray overscaling present in post discal and submarginal areas, rendering these areas lighter than the basal half of the wing. Dark brown rectangular macule at distal end of discal cell enlarged, approximately two to three times as wide as seen in nominotypical *auretorum* or *spadix*. Postmedian series of dark brown macules crescent-shaped, enlarged over those seen in nominotypical *auretorum* (Usually about twice the width), and edged distally with pale gray scaling. Submarginal series of dark brown macules obsolescent, but more developed than in spadix, in which they are usually absent. In nominotypical *auretorum* the submarginal series are usually very well developed. Outer margin edged with a thin brown line, fringe pale tan. Hindwing:

Ground color, macules, outer margin and fringe as forewing, except that postmedian series of macules are ovoid to rhomboid in shape. Pale orange "eyespot" mark in cell CU_1 CU_2 less developed than nominotypical *auretorum*, more prominent than in *spadix*, in which it is often obsolescent.

FEMALE. Size: forewing length 13.5–14.5 mm, mean 13.9 mm (N=6).

Dorsal surface. Forewing: Ground color dark brownish gray with a small area of dull fulvous scaling in the center of the wing. Fulvous scaling markedly reduced in extent from that seen in both other subspecies. In *spadix* the scaling often covers over one third of the wing and has relatively discrete borders, in nominotypical *auretorum* the scaling is usually extensive, but more diffused into the dark brown-gray ground color. Outer margin and fringe as in male. Hindwing: Ground color as forewing. Fulvous scaling absent, or present in small diffuse patch in the posterior half of the submarginal area. In *spadix* and nominotypical *auretorum* the fulvous scaling is usually present and more extensively developed. Ventral surface. Forewing and hindwing: Ground color and marking as in male.

TYPES. Holotype male: California, Los Angles County, Malibu Lake, 6 June, 1948, leg. Wm. T. Meyer. Allotype female: same data as male except 13 June, 1948. Paratypes (12 males, 5 females): 2 males same data as holotype, 1 male and 1 female same data except 16 June, 1948, 4 males same data except 13 June 1948, 2 males and 1 female same data except 17 June, 1948; 3 males, Malibu, 31 May, 1950, leg. E. R. Hulbirt; 1 female, Seminole Hill (Santa Monica mountains) 15 June, 1941, no leg; 1 female, No. of Hyw. 101, 1–1.5 mi. from Brent's Junction, 27 April 1989, leg. Robert Allen.

DEPOSITION OF TYPES. The type series except for the specimens of Allen and Pasko are in the collection of the Natural History Museum of Los Angeles county. The other paratypes will be placed in the Smithsonian Institution.

ETYMOLOGY. The name *fumosum* is derived from the latin root for smoke, in reference to the darkened, "smoky" appearance of this subspecies in contrast to both *S. a. auretorum* and *S. a. spadix*. The suggested common name for this butterfly is the Santa Monica Mountains hairstreak as all information indicate it is an endemic restricted to that range.

DISTRIBUTION AND PHENOLOGY. *Satryium auretorum fumosum* is thus far known only from the northern slopes and plateau of the western Santa Monica Mountains, where it presumably flies in a single brood from late April to June. The known distribution is illustrated in figure 2. The eastern part of the mountains have been intensively collected since the 1940's, including the detailed records of McFarland, without any evidence of the species. Scanty available information suggests flight usually occurs in June. The April record of the single female taken by Allen may reflect an adaptive response to

the early spring hot spell of 1989. This specimen was taken in a valley oak savannah at least one mile from potential foodplant, scrub oak, *Quercus dumosa*, which is the known foodplant of the subspecies *spadix*. The scrub oak is present in the other known localities of *fumosum* and is its likely foodplant. Scott (1986) cites two other oaks, *Q. lobata* and *Q. wislizenii* as hostplants.

A single female which is intermediate between *fumosum* and *spadix* was taken by John Pasko at Wildwood Park, Thousand Oaks, Ventura county, 5 June, 1980. The status of the population this specimen represents is insufficiently known.

DIAGNOSIS AND DISCUSSION. This subspecies is the darkest of the *S. auretorum* segregates and may represent an adaptive response to a moist coastal climate. It is readily distinguished from both *auretorum* and *spadix* by the dark ground color both dorsally and ventrally and by the more prominent series of ventral postmedian macules. A sample of all three subspecies are illustrated in figure 1, which permits comparison of the ventral shading and maculation character states among these segregates.

A somewhat similar phenotype is known from the Santa Ana mountains of Orange County. Three males specimens were examined, Silverado Canyon, 4 and 9 June, 1981, leg. Bob Iwahashi, collection of LACM. Several additional records from the same locality are given in Orsak (1977). These specimens were not examined. Because intervening habitat, the foothills of the San Gabriel mountains, are occupied by *spadix*, it is unlikely that the Santa Ana populations are monophyletic with *fumosum* even if they prove morphologically similar. Further systematic work is called for to clarify the matter, since this is the only known Santa Monica mountain endemic butterfly. Such research is urgent because of the great rate of land conversion in the area of both segregates and increasing fragmentation across their entire ranges.

The limited distribution of *fumosum* in a rapidly changing urban area indicate the subspecies should be considered for listing as threatened or endangered.

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Potential host range of *Spilosoma dalbergiae* (Moore) n. ssp. (Lepidoptera: Arctiidae) in India

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Abstract. The potential host range of *Spilosoma dalbergiae* (Moore) n. ssp. was determined by measuring feeding damage to pieces cut from leaves of 67 plant species and varieties, and was compared with literature reports of host range of other *Spilosoma* species. These tests indicated that *dalbergiae* is polyphagous, and has both horticultural and agricultural pest potentialities.

Introduction

A number of species of *Spilosoma* are engaged in the defoliation of a large variety of plant species of economic importance in North American, Afro-Asian, and European countries. In the oriental region, *S. obliqua* has been reported to cause serious damage to many crops (Patel, 1944, Anonymous, 1969; Prasad and Premchand, 1980). The taxa *Spilosoma dalbergiae*, *S. todara* and *S. bifascia* have been regarded as synonyms of *obliqua* (Lall, 1964). There are now reasons to believe that *obliqua* and *dalbergiae* are separate species (W. Thomas, personal communication), and in some instances damage attributed to *obliqua* might have been caused by *dalbergiae*.

The feeding behavior of larvae of *S. dalbergiae* n. ssp. is similar to *obliqua*. During early instars (I and II) larvae of *dalbergiae* n. ssp. feed gregariously on the leaf surface and do not move from plant to plant. In their advanced instars they move from plant to plant and from field to field, feeding on many plant species. The larvae may not restrict themselves to a particular habitat in later instars. The damage is done mainly by 3rd to 7th instar larvae, which skeletonize the plant.

There are several records of plants susceptibilities to *S. obliqua*, but most are based on observations of feeding damage. Bhattacharya and Rathore (1977) have published the host list of *S. obliqua* which contains 94 actual or potential hosts. However, host lists based on visual signs of damage provide no data concerning the influence of host plants

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on the feeding behavior of insect (Ladd, 1987). Many researchers have carried out feeding tests to obtain information on these aspects (Kogan and Goeden, 1970; Bhattacharya and Rathore, 1977).

The information on the host range of species can be utilized in the planning of the ecosystem for the establishment of an insect pest management programme. In the majority of ecosystems, agricultural and horticultural crops are surrounded by large tracts of uncultivated land. These areas harbor many plants which constitute a vital part of ecological niche of both pests and beneficial insects. In addition to providing protected sites during adverse conditions, such areas provide food to the insects when the fields are crop-free (Price and Waldbauer, 1982).

The purpose of this study was to determine the range of potential hosts of *S. dalbergiae* n. ssp. so that feeding behavior and pest potentiality could be quantified and susceptibility of ecosystem to it determined.

Materials and Methods

Taxonomy: The adults of *S. dalbergiae* and *S. obliqua* have been described by Hampson (1894) and Ahmad and Ahmad (1976) respectively. A complete description of the adults of this new subspecies will be published by Dr. W. Thomas (West Germany). Nominate *S. dalbergiae* is distributed in Kangra, Sikhim, Kasis and Nagas (Hampson, 1894), this new subspecies has been observed in Kangra and Pantnagar. *We provide here enough information to distinguish the immature stages of the two species.

The egg clusters of *dalbergiae* n. ssp. are not as compact as those of *obliqua*. The newly-hatched larvae of *dalbergiae* n. ssp. are yellowish, and the body is covered with tiny hair. A pink ring on the first abdominal segment, and pink spots on the last three segments, appear on the 2nd day. A dark black band on the first abdominal segment is apparent in the 2nd and 3rd instars, on a ground color of filthy yellow. The 4th, 5th and 6th instars are a dark and dirty yellow and possess a black band on the 1st abdominal segment. The dorsal part of the posterior segment is also black. The color of the 7th instar becomes dark and rusty.

In case of *S. obliqua*, the color of 1st instar is pale yellow and there are no pink bands or spots on the body. The second instar larva becomes yellowish with a greenish tinge, and there is no black band on the 1st abdominal segment. The color further darkens through the fourth instar. The thoracic segments and the three posterior abdominal segments develop a blackish tinge in the 5th instar, which remains until the last instar (Goel and Arun Kumar, 1983). The black band on the 1st abdominal segment of *S. dalbergiae* is not found in *S. obliqua* at any stage.

Culture: Adults were collected in a light trap. Paired insects were held for egg laying in plastic jars (diameter 9 cm; height 10.5 cm), the walls of which were lined with white paper. Adults were provided with a 10 percent sucrose solution soaked in cotton as food. The eggs obtained were kept in petridishes for hatching, and newly emerged larvae were reared under laboratory conditions (temperature: mean T min = 17.3°C; mean T max = 26.3°C; relative-humidity: mean RH min = 58.1% mean RH max = 93.7%) in glass jars (22 × 30 cm). The larvae were reared to fourth or fifth instar on the leaves of cowpea (*Vigna unguiculata* (L.) Walp.), which is known to be a good medium for rearing *S. obliqua*.

Host range test: The experiment was conducted in glass petridishes (12.25 cm diameter), the bottoms of which were filled with a 1 cm thick layer of wax. The surface of the wax was covered with blotting paper. Sixty seven cultivated or wild plant species were selected from various habitats (forest, horticultural, and agro-ecosystem) in Palampur (Himachal Pradesh). Each host was tested simultaneously in two petridishes. Four 1 cm square pieces were cut from the leaves of test plants and were fixed equidistant in the perimeter of each petridish with micro-entomological pins, 3 to 4 mm above the surface of blotting paper, so that larvae could feed freely on them. Before experimentation, the larvae were starved for 20 hours. One larva was released in the center of each petridish and was allowed to feed for two hours. The area of each leaf piece eaten by the larva was estimated using graph paper. Percent feeding on each plant species was calculated by taking the average of the 8 leaf pieces.

Results and Discussion

Feeding varied from 0 to 100 per cent among plant species (Table 1). In our opinion, the plants on which feeding was less than 5 per cent should not be included in the host spectrum of the species, since such low feeding rates may result from test bites by the insect, which may be taken even on non-host plants. So, the plants *D. gyrans*, *C. cajan*, *M. charantia*, *M. cochinchinensis*, *Z. mays*, *S. vulgare*, *L. esculentum*, *O. sativa*, *S. officinarum*, *P. purpureum*, *C. sinensis*, *J. regia*, *C. rotundus*, *C. nobilis* x *C. deliciosa*, *L. chinensis*, *Musa* sp., *C. medica* v. *galgal*, *E. japonica*, *O. europaea*, *M. indica*, *R. religiosa*, and *E. globulus* should not be included in the host list of *S. dalbergiae*.

Significant differences were noticed in the degree of feeding on different varieties of *G. max*; Punjab-1 was eaten more as compared to Bragg and Lee. Other Leguminous crops (i.e., *D. biflorus*, *P. sativum*, *P. vulgaris*, *P. mungo* and *V. unguiculata*) did not show any difference in percent feeding. Among Cucurbitaceous vegetables, *L. cylindrica* and *C. sativus* were eaten appreciably. As compared to other Solana-

Table 1: Host range of *Spilosoma dalbergiae* (Moore) n. ssp.

Test Plant	Family	Percent feeding	Test Plant	Family	Percent feeding
GROUP-1. AGRICULTURAL CROPS			GROUP-2. HORTICULTURAL AND FOREST PLANTS		
Glycine max (Punjab-1)	Leguminosae	97.63± 2.38	*Morus alba*	Moraceae	100.00± 0.00
Luffa cylindrica	Cucurbitaceae	87.50±12.54	*Bauhinia variegata*	Caesalpinoidae	94.88± 5.14
Cucumis sativus	Cucurbitaceae	73.01±21.31	*Prunus persica*	Rosaceae	79.38±16.42
Dolichos biflorus	Leguminosae	61.25±11.28	*Lantana camara*	Verbenaceae	75.00±25.07
Pisum sativum	Leguminosae	50.00± 0.00	*Malus domestica*	Rosaceae	74.25± 0.75
Solanum melongena	Solanaceae	48.50± 1.50	*Fragaria ananassa*	Rosaceae	72.50±11.79
Phaseolus vulgaris	Leguminosae	43.50± 4.50	*P. amygdalus* v. *dulcis*	Rosaceae	64.88± 8.15
Cucurbita pepo	Cucurbitaceae	40.75±13.79	*Salix babylonica*	Salicaceae	57.13±20.94
Phaseolus mungo	Leguminosae	38.25±11.79	*Amomum subulatum*	Zingiberaceae	53.25± 3.26
Brassica campestris v. *sarson*	Cruciferae	35.63±12.91	*Robinia pseudoacacia*	Leguminosae	52.25±47.89
B. oleracea v. *capitata*	Cruciferae	30.00± 5.01	*Ficus carica*	Moraceae	50.00±50.15
Spinacia oleracea	Chenopodiaceae	29.50± 4.51	*Pyrus communis*	Rosaceae	48.25± 0.75
Ricinus communis	Euphorbiaceae	24.63± 5.39	*Lagerstroemia indica*	Melastomaceae	38.00± 9.03
Abelmoschus esculentus	Malvaceae	23.88± 5.39	*Prunus domestica*	Rosaceae	37.63±37.49
Vigna unguiculata	Leguminosae	23.13± 0.63	*Punica granatum*	Myrtaceae	36.13± 1.13
Colocasia esculenta	Araceae	20.88± 2.88	*Rosa indica*	Rosaceae	29.50±29.59
G. max (Lee)	Leguminosae	20.63±20.69	*Populus* sp.	Salicaceae	21.50±21.56
Raphanus sativus	Cruciferae	20.62± 0.63	*Cannabis sativa*	Moraceae	19.25±19.31
G. max (Bragg)	Leguminosae	17.25± 6.27	*Grewia* sp.	Tiliaceae	17.13±16.93
Cajanus cajan	Leguminosae	13.50±13.04	*Carya illinoensis*	Juglandaceae	12.38± 4.64
Amaranthus spinosus	Amaranthaceae	10.00± 4.01	*Psidium guajava*	Myrtaceae	9.75± 9.78
Solanum tuberosum	Solanaceae	9.38± 9.40	*Citrus limon*	Rutaceae	6.63± 0.13
Capsicum sp.	Solanaceae	8.25± 1.50	*Camellia sinensis*	Theaceae	4.63± 1.38
Desmodium gyrans	Leguminosae	3.00± 1.00	*Juglans regia*	Juglandaceae	4.50± 4.51
Capsicum annum	Solanaceae	2.88± 0.13	*C. nobilis* x *C. deliciosa*	Rutaceae	4.00± 0.00
Momordica charantia	Cucurbitaceae	1.00± 1.00	*Litchi chinensis*	Sapindaceae	2.63± 2.63
Mucuna cochinchinensis	Leguminosae	0.12± 0.13	*Musa* sp.	Musaceae	0.75± 0.75
Zea mays	Graminae	0.00± 0.00	*C. medica* v. *galgal*	Rutaceae	0.25± 0.25
Sorghum vulgare	Graminae	0.00± 0.00	*Eriobotrya japonica*	Rosaceae	0.00± 0.00
Lycopersicum esculentum	Solanaceae	0.00± 0.00	*Olea europaea*	Oleaceae	0.00± 0.00
Cyperus rotundus	Cyperaceae	0.00± 0.00	*Mangifera indica*	Anacardlaceae	0.00± 0.00
Oryza sativa	Graminae	0.00± 0.00	*Ficus religiosa*	Moraceae	0.00± 0.00
Saccharum officinarum	Graminae	0.00± 0.00	*Eucalyptus globulus*	Myrtaceae	0.00± 0.00
Pennisetum purpureum	Graminae	0.00± 0.00			

ceous vegetables tested, *S. melongena* was eaten more. No significant difference was seen in feeding among Cruciferous vegetables.

Temperate fruits were consumed more as compared to sub-tropical fruits; however, no significant differences existed among different pome, stone, or nut fruits. Other temperate fruits like *F. ananassa* and *P. granatum* were also eaten appreciably while *O. europaea* was rejected. Percent feeding was very low on all the sub-tropical fruits tested. Appreciable feeding occured on some other plants of this group also. Maximum feeding occured on *M. alba* followed by *B. variegata* and *L. camara*.

Comparison of the host range of different species of *Spilosoma* indicates that various plant species such as *A. esculentus*, *B. campestris* var. *sarson*, *C. cajan*, *C. sativa*, *C. sativus*, *D. biflorus*, *L. camara*, *L. cylindrica*, *P. mungo*, *S. oleracea* and *V. unguiculata* are eaten by both the Oriental species, *obliqua* and *dalbergiae*. *S. dalbergiae* also has some hosts like *C. pepo*, *P. vulgaris*, *P. domestica* and *P. persica* common with the North American species *S. virginica*. *G. max*, *P. sativum*, *R. sativus*, *R. communis*, *S. melongena*, *S. tuberosum*, and *B. oleracea* var. *capitata* are hosts of *S. dalbergiae*, *S. obliqua* and *S. virginica*. *M. alba* has been found to be a host of many *Spilosoma* species, including *dalbergiae*, *obliqua*, *imparilis*, *lubricipeda*, *mori* and *subcarnea* (Maki, 1916; Fenton, 1937; Golanski, 1967; Tietz, 1972; Bhattacharya and Rathore, 1977; Roberts et al., 1977; Hondo, 1981).

S. dalbergiae and *S. obliqua* (Bhattacharya and Rathore, 1977) showed several similarities and differences in their host preference. Both these species rejected *M. charantia*, *M. indica*, *F. religiosa*, *O. sativa* and *S. officinarum*. *S. dalbergiae* ssp. n. accepted the plants *P. granatum*, *S. tuberosum* and *F. carica*, which are rejected by *S. obliqua*. This species rejected *C. rotundus* and *Z. mays*, which are accepted by *S. obliqua*. The plants *C. sativus* and *S. oleracea* were found to be good host plants for both species. Neither species preferred *P. guajava*.

The wide range of acceptable hosts clearly indicates that the new subspecies of *dalbergiae* is polyphagous. The tendency of the insect to feed on temperate fruits (e.g., almond, apple, pear, peach, plum, and strawberry), vegetables (e.g., pumpkin, vegetable sponge, cucumber, brinjal, potato, radish, cabbage, mustard, lady-fingre, and spinach), and legumes (e.g., pea, black gram, French bean and soybean) indicates that the species has both horticultural and agricultural pest potentialities. It also readily accepted many forest and ornamental plants. We cannot rule out the possibility that some of the out-breaks recorded for *obliqua* (Lall, 1964) might have been caused by *dalbergiae*. The tendency of *dalbergiae* to feed on a wide variety of plant species indicates that the insect can be a pest in many ecosystems.

The spectrum of potential host plants of early and advanced instars of larvae may vary. Generally, the spectrum of potential host plants have been found to be wider for early instars than for old larvae (Wiklund,

1973). The host range of this new subspecies indicates that it can survive well in agricultural, forest, or mixed systems. The ability of the species to feed on seasonal, annual, biennial, perennial, herbs, shrubs, or trees indicate its substantial potential as a pest species.

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The life-history of *Tomares ballus* (Fabricius, 1787) (Lepidoptera: Lycaenidae): phenology and host plant use in southern Spain

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Abstract. The life-history of *Tomares ballus* in southern Spain is described. In Sierra Morena *T. ballus* is monophagous and feeds on flowers and fruits of *Astragalus lusitanicus* (Lam., 1783) (Fabaceae), despite the availability of other potential host plants. The phenological coupling between *T. ballus* and *A. lusitanicus* is considerable in Sierra Morena, whereas the flowering period of the remaining potential host plant species is approximately one month later. In the Guadalquivir Valley butterflies show preferences for *Medicago polymorpha* (L., 1753). Other aspects of the life-history of *T. ballus* are discussed in relation to the morphological and productive features of *A. lusitanicus*.

Introduction

Tomares ballus is a Mediterrranean biogeographical component of the Palaearctic butterfly fauna. It is frequently found in some parts of North Africa, the southeastern half of the Iberian Peninsula and a small region in southeastern France, feeding mainly on *Lotus hispidus* (D.C., 1805) (Higgins & Riley, 1980). The other species of the same genus flying in Europe is *T. nogelli* (Henrich-Schaffer, 1851), which flies in Rumania and uses *Astragalus ponticus* (Pallas, 1800) as host plant (Higgins & Riley, 1980). In northern Africa the range of *T. ballus* overlaps that of *T. mauretanicus* (Lucas, 1849) which feeds on *Hippocrepis multisiliquosa* (L., 1753) (Higgins & Riley, 1980; Courtney, 1983).

Despite the recent work by Descimon and Nel (1986), *T. ballus* is not a well known species. The present work focuses on different aspects of the life history of *T. ballus* and its host plants in southern Spain.

Study Area

Field work was carried out in areas located on both sides of the middle of the Guadalquivir River in southern Spain (Córdoba province) (Fig. 1). In the northern zone (Sierra Morena Mountains, SM), soils are mainly siliceous and poorly-developed. A varying degree of human management has affected the composition and structure of the original vegetation. The region is a mosaic of different units, where areas of oak forest *(Quercus rotundifolia* and *Q. suber)*

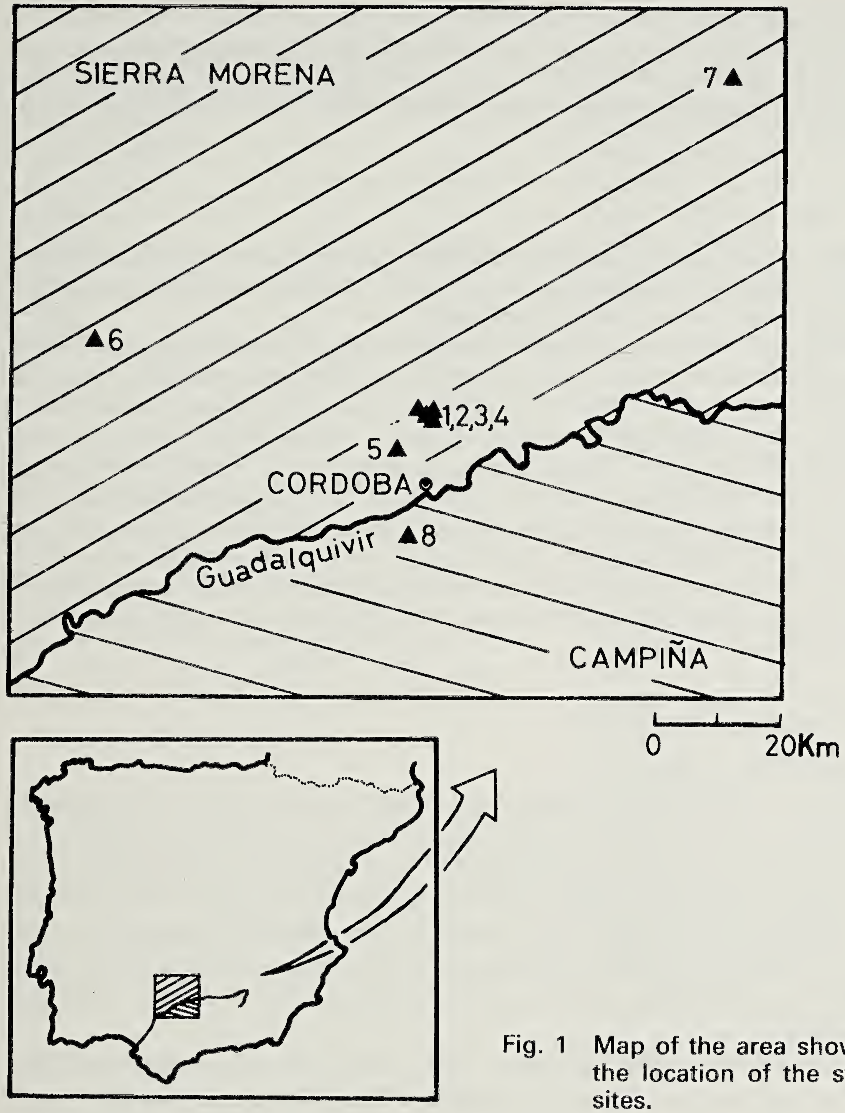

Fig. 1 Map of the area showing the location of the study sites.

alternate with scrubland or therophytic pastureland. Scrubland is mainly composed by Cistaceae (*Cistus ladanifer, C. monspelliensis, C. salvifolius*), Labiatae (*Rosmarinus officinalis, Lavandula stoechas*) and Ericaceae (*Arbutus unedo, Erica arborea*). A more detailed description can be found in Gonzalez Bernaldez et al. (1976). Seven different study sites (1-7) were choosen in this area (Fig. 1).

The deep and fertile calcareous soils of the southern zone, located in the Guadalquivir Valley (Campiña, CA), have allowed an intensive agricultural exploitation. The original vegetation has been completely removed and replaced by herbaceous crops (wheat and sunflowers) and olive groves. Only one site (8) was choosen in this area (Fig. 1).

The study area has a Mediterranean climate (Ashmann, 1973) which influences the phenology and growth rhythm of both vegetation and fauna. In the year of our field research (1986) the annual rainfall was 532.5 mm, a figure well below the long-term average annual rainfall for the area (x = 657 mm, n = 21 years).

Methods

Most of the data concerning the life-history of the species were obtained from larvae collected in the field and reared in the laboratory or hatched from eggs laid by females in insectaries (net-cages).

Different patches of *A. lusitanicus* (located in sites (1-6) were selected for field measurements. A total of 108 *A. lusitanicus* plants were randomly tagged in early February, when they were just resprouting. These plants were examined weekly; their height and number of stems, inflorescences and buds were recorded. At the end of the growing season (June), the numbers of fruits and viable seeds were also counted. To evaluate the other potential food plants for their frequencies, flowering phenology and flower availability in the first zone (SM), we established five permanent line transects, each one with six quadrats of 50 × 50 cm spaced at 1.50 m intervals. The number of inflorescences for each herbaceous plant species were counted in the 30 quadrats every fifteen days from February to June.

Results and Discussion

1. *Use of host plants.*

Since *T. ballus* uses a wide range of species belonging to Fabaceae as host plants throughout its distribution range (Jordano & Rodriguez, 1988), this butterfly can be classified as oligophagous (Slansky, 1974; Wiklund & Ahrberg, 1978; Scriber & Slansky, 1981). For example, Descimon & Nel (1986) have reported five different foodplants in the same area in SE France (*Medicago truncatulata, Anthyllis tetraphylla, Hippocrepis unisiliquosa, Onobrychis caput-gallii* and *Lotus ornithopodioides*).

In the Campiña area (CA) and other areas of the Guadalquivir River Valley where *A. lusitanicus* is absent, *M. polymorpha* is the host plant for *T. ballus*. This species is a common papilionaceous legume growing in ditches, river banks and abandoned olive groves. This area (CA) contains a lower number of potential host plant species than pasturelands of the Sierra Morena Mountains (SM).

All oviposition records during 1986 from the CA population were on *M. polymorpha*, despite the fact that *M. sativa* L. was also available, but less abundant. At the time of maximum butterflies density, no *M. sativa* plants with flowers or buds were found.

Eggs are laid on the leaves of *M. polymorpha* usually on the upperside (80%, n = 24), and in many cases on plants still without flowers. Despite the abundance of *M. polymorpha* in this zone, where it forms extensive dense patches, considerable overspread egglaying is exhibited (distance between two successive egglayings x = 12.3 ± 14.5 m, max. = 49.5, min.

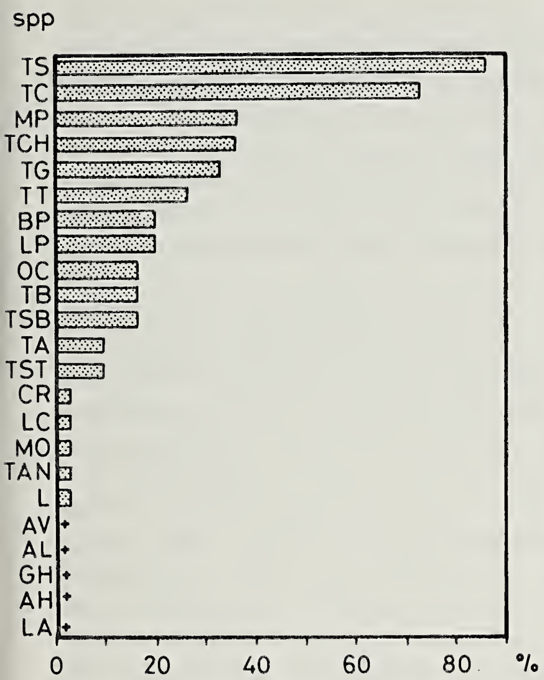

Fig. 2 Frequency of appearance (%) of potential host plants species in therophytic pastureland in SM. Measurement was made using thirty 50 × 50 cm quadrats in sites 1 – 3. Abbreviations: TS = *Trifolium striatum*. TC = *T. campestre*, MP = *Medicago polymorpha*, TCH = *T. cherleri*, TG = *T. glomeratum*, TT = *T. tomentosum*, BP = *Biserrula pelecynus*, LP = *Lotus parviflorus*, OC = *Ornithopus compressus*, TB = *T. bocconei*, TSB = *T. subterraneum*, TA = *T. arvensis*, TST = *T. stellatum*, CR = *Coronilla repanda*, LC = *Lotus conimbricensis*, MO = *Medicago orbicularis*, TAN = *T. angustifolia*, L = *Lathyrus sp.*, AV = *Anthyllis vulneraria*, AH = *A. hamosus*, AL = *Astragalus lusitanicus*, GH = *Genista hirsuta* and LA = *Lupinus angustifolius*, + = species present in the study area but not in the quadrats. The last three species are perennial herbaceous or woody plants with a bushy appearance. Its quantification requires a different sampling method.

= 2, n = 15). Moreover, eggs are usually laid singly. Only one oviposition event of three eggs on a single plant and another of two eggs were observed. This isolated egg-laying pattern is consistent with the one reported by other authors (Nel, 1984; Descimon and Nel, 1986).

The colonies of *T. ballus* in Sierra Morena (SM, study sites 1-7) are restricted in host plant usage, feeding on *A. lusitanicus* despite the availability of different potential host plants (Fig. 2). In 1986, a total of 1962 eggs were counted on *A. lusitanicus* and only one on *Ornithopus compressus*.

Most eggs are laid between the buds of incipient inflorescences (91.13%, n = 1962), but females occassionally lay them on apical or mature leaves or on the main stems of plants. Several are often found on

the same inflorescence, but not in clusters as does *T. mauretanicus* (Courtney, 1983). Eggs of different age (recognizable through the variable color of them, from pale green to dark grey) are frequently found on the same inflorescence. Thus, plants can receive considerable egg loads, up to a maximum of 38 eggs recorded for a single stem. This egg-laying behaviour differs from the single egg oviposition, quite common in Lycaenidae, and is surprising for a species whose caterpillars have been described as cannibalistic (Nel, 1984; Descimon & Nel, 1986).

A. lusitanicus is a perennial herbaceous plant whose distribution includes the southwest of the Iberian Peninsula and the northwest of Africa. Plants show a variable number of vigorous and erect stems ($x = 7.0 \pm 5.02$, $n = 108$) which grow up to 90 cm high ($x = 55.8 \pm 14.1$ cm, $n = 108$). Stems resprout yearly from a woody root. Leaves are pinnate and 8-12 cm long. Stems produce numerous conspicuous inflorescences ($x = 6.5 \pm 2.0$, $n = 108$) of dense white flowers in racemes. The average number of floral buds per inflorescence is 17.7 ± 13.2 ($n = 108$). Fruits are legumes approximately 10 cm long (Polunin, 1982) and dehisce when ripening. Each stem produce an average of 7.5 ± 10.0 ($n = 108$) mature fruits. Ripe fruits produced an average of 11 seeds ($n = 100$), with only 22.4% being viable and the remainder being aborted. The appearance of *A. lusitanicus* is quite different from that of the remaining potential host plants, since all of them are procumbent small herbaceous plants.

This *Astragalus* species is toxic for livestock (Gonzalez Rodriguez, 1980) especially for sheep (Moyano, 1985) but the compound responsible of this toxicity is unknown (Infante et al., 1964; Poyato, 1968; Baraibar, 1982). Thus, plants are avoided by vertebrate herbivores (*Cervus elaphus*, *Oryctolagus cuniculus*), which clearly benefits *T. ballus* survivorship in the SM population, whereas grazing and trample may cause high mortality to larvae feeding on *M. polymorpha* in the CA population. The effects of *A. lusitanicus* alellochemicals on SM *T. ballus* population remain unassessed.

A. lusitanicus grows vigorously following particular shrub vegetation management practices (e.g. fires, plowing). On the other hand, it is scarce in areas with considerable shrub and tree cover. This fact suggests that the suitability of *A. lusitanicus* patches to *T. ballus* colonies may decrease through the years and finally disappear if additional disturbance does not occur; that is, *A. lusitanicus* is a successional or even a fugitive species.

2. *Life history of T. ballus.*

Eggs are roughly spherical with average diameter of 0.54 ± 0.01 mm ($n = 115$). The average weight is 0.0007 ± 0.0005 g ($n = 151$). Our data does not allow to establish any relationship between egg weight and female age, as happens in different satyrid butterflies (Wiklund and

Karlsson, 1984; Karlsson and Wiklund, 1985). Hatching usually occurs ten days after oviposition. New caterpillars make a hole in the bud where the egg was laid or across the petals (in the case of an unopened flower). Feeding occurs inside the bud. Caterpillars, described in detail by Chapman (1904), are adapted to an endophytic life, feeding on anthers and ovaries during their early stages. Sometimes several caterpillars have been found in the same flower.

As flowering progresses, caterpillars feed on the developing seeds within the fruits. In order to reach the seeds, they make a hole through the fruit valve which is plugged with silk from the inner side. In this manner, caterpillars can consume several fruits before finishing their development. The high number and size of inflorescences and fruits of *A. lusitanicus* allow the development of several caterpillars on the same plant without apparent problems of competition or cannibalism (Jordano, 1987).

Some authors have pointed out a possible mutualistic relationship between this species and ants (Martin Cano, 1982). *T. ballus* caterpillars have three types of specialized organs: porous cupola glands, eversible tentacles and Newcomer's gland (Martin Cano, 1982). Observations made with a scanning electron microscope confirm the presence of these organs in *T. ballus* larvae (Jordano, unpubl.). However, we have never observed any type of interactions between this species and ants in the study area. This supports the observations made by Descimon and Nel (1986). In spite of this, caterpillars and pupae introduced in artificial nests of *Cataglyphis hispanica*, a carnivorous ant species, were not attacked by the ants (Jordano, unpubl.), as happens with *Artogeia rapae* larvae.

During 1985, twenty five third and fourth instars larvae were collected in the field. Of them, 36% showed evidence of attack by parasitoids. Every parasitized larvae contained a considerable number of parasitoids ($x = 16.8 \pm 6.2$, $n = 8$) belonging to an undescribed species of a small wasp of the genus *Cotesiia* (Braconidae, Microgastrinae, Cotesiini). Parasitoids killed the larvae within 4-7 days. During this time, larvae lost on the average 48.8% of their weight ($n = 9$). The endophytic habits of larvae and their specialized feeding behavior, likely provide some protection against parasitoids. The larvae are exposed to parasitoid attacks only when they have to move from one consumed flower or fruit to another.

The larvae of the wasps parasitoid come outside the caterpillars to pupate in small cocoons and imagos emerged during the same spring. Therefore they have more than one generation per year and probably are not specific to *T. ballus*.

Larval development of *T. ballus* lasts about two months in laboratory conditions with no precise light or temperature regulation ($x = 58.1 \pm 3.5$ days, $n = 18$). Males and females have development periods of similar lengths.

Caterpillars reach a maximum weight over 0.30 g (female max. weight = 0.40 g; male max. weight = 0.35 g). However, weight losses occur after reaching maximum weight during prepupal phase, during which larvae stop feeding. In the prepupal phase caterpillars leave the plant on which they have developed, searching for a place to pupate. As a result, the final weight of caterpillars before pupation is considerably lower than their maximum weight, ranging between 0.20-0.25 g (females max. final weight = 0.26 g; males max. final weight = 0.24 g). Weight loss during the prepupation phase was about 30% of maximum weight ($x = 30.4\% \pm 7.6$, $n = 12$).

Pupation occurs in the soil, generally partially buried or under stones. Pupae are brown without rugosities or maculations. We did not find any myrmicophilous or sound producing organs. In a random sample of pupae obtained in the laboratory, females were found to weigh significantly more than males (females, $x = 0.17 \pm 0.02$ g, $n = 27$; males, $x = 0.14 \pm 0.03$ g, $n = 27$; $F = 10.94$, $p < 0.01$).

Diapause occurs in the pupal stage and imagos emerge the following year. Notwithstanding, some pupae did not produce imagos, continuing in diapause and giving imagos two years later. This fact suggests that a cold exposure for interrupting diapause might be necessary, as has been reported for other species (Templado & Alvarez, 1985).

Female butterflies were larger (CVL mean = 15.85 ± 1.07, $n = 8$; WS mean = 29.30 ± 1.60 mm, $n = 6$) than males (CVL mean = 14.38 ± 0.67 mm, $n = 9$; WS = 27.70 ± 1.32, $n = 9$) (CVL = costal vein length, WS = wing span).

Longevity of imagos in the field has not been assessed, but it ranged between 18 and 22 days in insectaries.

Potential female fertility was approached by dissecting the abdomen of virgin butterflies just emerged from the pupae and counting their eggs and oocytes (Dunlap Pianka et al. 1977; Ehrlich & Ehrlich, 1978; Dunlap-Pianka, 1979). Values ranged between 317 and 584 eggs per female ($x = 456.2 \pm 102.0$, $n = 5$).

3. *Phenology.*

T. ballus is univoltine and one of the first species which can be seen every year at the study area, excluding those which spend the winter as imagos (eg. *Gonepteryx rhamni, G. cleopatra* and *Nymphalis polychloros*). It is on the wing from early February until the end of April, with a peak flight around mid-March. Slight between-year variations are observed, depending on weather conditions. Isolated individuals have been observed as early as the end of January and as late as May.

Data of study sites 1–3 displays the flowering phenology of the potential host-plant species living in the same zone as *A. lusitanicus* (Fig. 3). The flowering period of the latter species occurs earlier than that of the remaining ones except for *Trifolium subterraneum* (whose flowering and underground ripening characteristics excludes it as a suitable host plant).

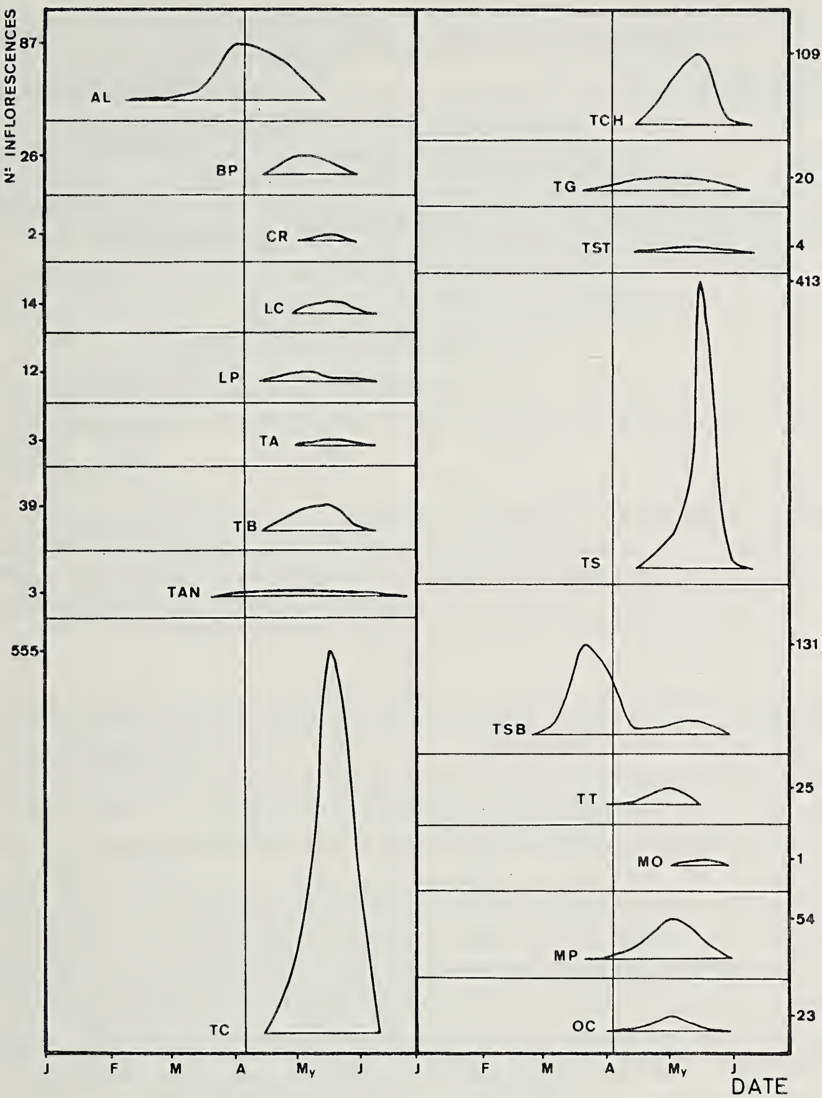

Fig. 3 Flowering phenology of potential *T. ballus* host plants (Fabaceae) growing in the study area. Inflorescences were counted in thirty 50 × 50 cm quadrats every fifteen days. The central line on the graphs show *T. ballus* egg laying peak. Notice the phenologycal coupling between *T. ballus* egg laying peak. Notice the phenologycal coupling between *T. ballus* and *A. lusitanicus* and in a lesser extent with *T. subterraneum*. Abbreviations as in Fig. 2.

Figure 4 shows the comparative phenology of *T. ballus* and of *A. lusitanicus* at the study area (SM). The flight period of *T. ballus* and, more specifically, its maximum egg laying activity, is coincident with the flowering peak of *A. lusitanicus* (Jordano, 1987), whereas the flowering peak of the remaining potential host plants occurs at least one month later (Fig. 3). This is the case of *Anthyllis tetraphylla* (the main

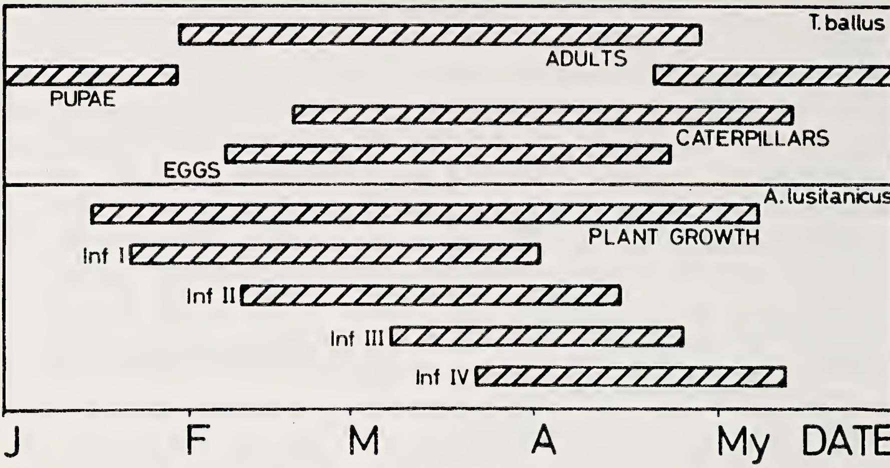

Fig. 4 *T. ballus* and *A. lusitanicus* phenology. Plant growth includes from plant resprouting until the end of the biomass increase. Inf I: Inflorescences with floral buds (petals not visible). Inf II: Inflorescences with floral buds and closed flowers (petals visible). Inf III: Inflorescences with open flowers. Inf IV: Inflorescences with fruits.

host-plant in SE France) and *M. polymorpha* (the host plant for the Guadalquivir Valley population, CA) (Fig. 3). These time lags account for the restricted monophagous strategy of *T. ballus* at the SM population, since the caterpillars feed on flowers during their earlier instars.

At Sierra Morena, (SM), *T. ballus* practices monophagy with relevant behavioral and ecological relationships with its host plant, *A. lusitanicus*. The patches of this species are easy to locate for ovipositing females due to their spatial and temporal predictability. At the same time, its high flower and fruit production allow the successful development of several *T. ballus* larvae on a single plant. Therefore, it can be considered as the most suitable host plant used by the butterfly locally. In this way, herbaceous terophytic legumes could be considered as secondary hosts in areas where *A. lusitanicus* is absent.

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Notes

Temporary breeding populations of *Phoebis sennae eubule* (L.) (Lepidoptera: Pieridae) in Ohio and West Virginia

The cloudless sulphur, *Phoebis sennae* (L.) is primarily a tropical and subtropical butterfly. In eastern North America, the subspecies *P. s. eubule* (L.) is a permanent resident generally south of North Carolina, Tennessee and Arkansas. The species regularly emigrates northward in late summer and early autumn, occasionally reaching southern Canada (Opler and Krizek, 1984; Scott, 1987). Northward, the species occurs in the Mississippi Valley to central Illinois (Irwin and Downey, 1973) and along the Atlantic Coastal Plain to New Jersey (Stone, 1903; Shapiro, 1966). In these areas, it is known to reproduce as far north as west-central Illinois (Sedman and Hess, 1985) and Virginia (Clark and Clark, 1951). Northern breeding records of *P. s. eubule* from outside the Mississippi Valley and Atlantic Coastal Plain are virtually nonexistant.

In 1987, much of the eastern United States witnessed a large and previously unsurpassed flight of *P. s. eubule*. Numbers were observed as far north as Wisconsin and New York. It was common in portions of Missouri, Illinois and Kentucky and frequently encountered in Indiana, Ohio and West Virginia. The species was unusually common even in the extreme southeastern states where it is a permanent resident.

In Ohio, historical records of *P. s eubule* were limited to only eight counties following over 130 years of collecting. During the exceptional flight of 1987, the species was recorded in 15 additional counties and observed in at least eight others. In West Virginia, *P. s. eubule* was recorded in seven counties, representing the first records in the state. Individuals were observed and captured as early as April and May in this region. Prior to 1987, the earliest date of capture in Ohio was 29 July (1931).

Several temporary breeding populations of *P. s. eubule* were found in Ohio and West Virginia in 1987. Many of these populations were located directly adjacent to rivers and streams. Valleys of rivers and major streams appear to serve as primary corridors of dispersal for this species in the region. A riparian affinity has also been noted in Illinois (Sedman and Hess, 1985). In West Virginia, *P. s. eubule* was observed at the summit of Cheat Mountain (approx. 1140 m.), thus it is possible that the species also follows mountain ridgetops.

Two color forms of *P. s. eubule* larvae were found and reared on wild senna (*Cassia hebecarpa* Fern.) and partridge-pea (*Cassia fasciculata* Michx.). Where the butterfly utilized wild senna in Ohio, green larvae were found feeding on both the leaves and yellow flowers of the plants. Conversely, yellow larvae were nearly always found feeding on the flowers. Because of these color associations, even large mature larvae were inconspicuous. Pupal periods of the species in Ohio and West Virginia ranged from five to nine days, in contrast to the reported pupal periods of *P. s. eubule* in Georgia (10–12 days) (Scudder, 1889) and *P. s. marcellina* in Brazil (nine–13 days) (Brown and Heineman, 1972). The finding may suggest that development is more rapid where the species is not a permanent resident.

At least two broods of *P. s. eubule* were produced in Ohio and West Virginia in

1987. The populations persisted until the hostplants began to dry in late summer. Adults, especially males, continued to be observed into late September. No southward autumn migration was reported, though such an occurrence was noted in Tennessee in September (L. Martin, pers. comm.). Because the flight of *P. s. eubule* is typically rapid and unflagging, many more individuals were observed than collected. However, males are strongly attracted to bright yellow objects and many were captured using decoys of yellow paper and dried specimens of the species.

Exactly what caused this unprecedented explosion of *P. s eubule* is unknown. Surely, no single factor can be attributed, but climatic conditions probably played a major role. In much of the east, the winter of 1986–87 was mild and followed by an early spring. This may have allowed *P. s. eubule* to begin reproducing and emigrating prematurely, thereby reaching northern areas early in the season and establishing breeding populations. An early arrival in the north may also have been augmented by overwintering individuals. If *P. s. eubule* adults have the ability to overwinter, as suggested by Scudder (1889), it could have survived far to the north of its permanent range during the mild winter of 1986–87. These factors alone, however, do not explain the overall abundance throughout much of the east.

It was also noted in 1987 that the hostplants, especially partridge-pea, experienced a very productive year in Kentucky, Ohio and West Virginia. If the situation was widespread in the east, it could have provided the necessary catalyst for the rapid spread and increased productivity of *P. s. eubule* in this portion of the country. An abundance of partridge-pea was observed in connection with a local outbreak of *P. s. eubule* in Kansas in 1987 (Howe, 1987).

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Thanatosis in the Neotropical Butterfly *Caligo illioneus* (Nymphalidae: Brassolinae)

During the course of studies on flight kinematics in Neotropical butterflies, thanatosis (death-feigning behavior) was noticed in a female *Caligo illioneus*. The following observations were made in July 1987 in a small screened insectary on Barro Colorado Island, Republic of Panama. Mass of the insect was 1.84 g, the ambient air temperature was 27°C, and the relative humidity 88%. Ambient air motions in the insectary were negligible. Observations began with the butterfly at rest on an insectary wall with the wings folded together dorsally. When grasped by the base of the folded forewings and removed from the wall, the butterfly entered a thanatonic condition, characterized by complete absence of wing or leg motion, with the legs tucked against the body as in flight. When then placed upon (and with wings parallel to) a horizontal surface, the insect remained motionless. While in this condition, tactile stimulation of the wings, legs and body produced no behavioral response. Eventually the insect righted itself and flew away; in eight consecutive trials each separated by several minutes, the mean time to self-righting was 55 seconds (s.d. = 49 s). Dropping the thanatonic insect upside-down from a height of several meters resulted in a short vertical drop followed by wing-spreading and active flapping flight or gliding to the walls of the insectary.

Thanatosis has been observed in a variety of animals, including numerous beetles (Bleich, 1928), mantids (Edmunds, 1972), moths (Blest, 1964), snakes (Gehlbach, 1970; see also Greene, 1988) and mammals (e.g. Francq, 1969; Ewer, 1966). It has been suggested that thanatosis induces relaxation of predator attention, possibly allowing for active escape of the prey during the handling phase of a predatory event (Ratner & Thompson, 1960). Butterflies are frequently attacked by insectivorous birds. Chai (1986) reported that the jacamar *Galbula ruficauda*, a specialized avian predator of flying insects, required on average 9 minutes (maximally 40 minutes) to strip large butterflies of their wings prior to consumption of the body. Wing-stripping by jacamars occurs upon the cessation of struggle by the butterfly. If thanatosis on the part of butterflies does induce momentary inattention during the wing-stripping procedure, possibilities for escape are heightened. Additionally, death-feigning may be an advantageous defense, following an initial unsuccessful attack, against predators which only attack moving prey. Curiously, thanatosis involves an inhibition of wing flapping concurrent with an absence

of tarsal contact with a substrate. In general, loss of tarsal contact initiates wing flapping responses in insects (see Chapman, 1971). Neural reflexes which ordinarily would initiate flight must therefore be facultatively suppressed during the thanatonic condition.

It was unfortunately not possible to obtain additional specimens of *Caligo illioneus* to evaluate in detail various physiological and behavioral aspects of thanatosis. However, the present results are unlikely to be anomalous, as DeVries (*pers. comm.*) has observed thanatosis in three papilionid species (*Parides arcas, P. childrenae*, and *P. erithalion*), in a *Lycorea* sp. (Danainae), and in several ithomiine genera. Thanatosis may thus be a widespread antipredatory defense in tropical butterflies.

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A New Specimen of *Vanessa braziliensis* "ab. *dallasi*" (Nymphalidae) from Argentina

Vanessa braziliensis (Moore) "ab. *dallasi*" was described and figured by Koehler (1945, p. 256; pl. 20, fig. 2). The "cotypes" (apparently at least two specimens) are stated to be from the Sierra de Ambato, Province of Catamarca, Argentina, at 2000 meters. In addition to the color plate, I have examined the "cotype" in the Breyer collection at the Museo de La Plata. The labels of the "cotypes" of this and *Vanessa carye* "ab. *bruchi*," described in the same paper,

Fig. 1. *Vanessa braziliensis:* "ab. *dallasi*" (above) and normal (below), upper and lower surfaces, San Miguel de Tucumán, Argentina, 29.XI.1989.

appear to have become interchanged at some point, but both specimens bear the same label data, "Los Angeles (Capayán), 1800 m, I.1941." Los Angeles and Capayán are two towns a few km NW and S of San Fernando del Valle de Catamarca, the provincial capital, respectively.

It is evident that "ab. *dallasi*" is extremely similar to "ab. *ahwashtee*" Gunder of the closely-related *V. virginiensis* Drury, and "ab. *bruchi*" is nearly identical to one phenotype in the "*letcheri-muelleri*" series of aberrations in *V. annabella* Field. Just as these aberrations are not very rare in *V. annabella*, similar aberrant specimens of *V. carye* exist in most major Argentine collections and I have taken several myself. In *V. virginiensis*, specimens of "*ahwashtee*" are very rare (Shapiro 1983). Likewise, other than the "cotypes," no captures of *V. braziliensis* "*dallasi*" have been reported or located in Argentine collections.

A male nearly identical to the La Plata "cotype" was captured by me on 29 November 1989 in a vacant lot in San Miguel de Tucumán, Argentina in the company of numerous normal specimens (fig. 1).

Koehler was familiar with the European literature of temperature-induced aberrations, and confidently attributes all the cases of "melanism" described in his paper to "passing strong nocturnal cooling.... Some frost of near frost, acting on the young chrysalids has produced the specimens in question."

Koehler's explanation may be valid (Shapiro 1973, 1975), but it is extremely unlikely that several similar aberrations of two different species would be collected in the same locality on the same day. The possibility that the specimens were actually produced experimentally cannot be ruled out. Indeed, such practices ultimately gave the study of shock phenotypes a bad reputation in Europe.

The Tucumán specimen was collected in the subtropical lowlands, where no local cold shocks were likely. The weather records for Tucuman do not indicate any unusual temperatures in the previous two months. However, *V. braziliensis* is highly mobile and like *V. carye* in the same region appears to undergo regular seasonal altitudinal migration. At the time of this collection, individual immigrant *V. braziliensis* could be seen moving upslope and colonizing the Sierra de Aconquija and Cumbres Calchaquies west of Tucumán, up to 4000 m. This movement coincides with the first seasonal rains of the "Bolivian winter," before which host plants are not available in the highlands. The seasonality thus argues strongly against this individual having bred in the cold mountains and descended to the lowlands, unless it had taken part in the downslope migration five or six months before.

This is the first aberration I have seen among many hundreds of *V. braziliensis* in 12 years of field work in Argentina. It is a very powerful testimony to the conservatism of this series of apparently homologous aberrations, which seem to occur throughout not only *Vanessa* but the closely allied genera as well.

I thank the Museo de La Plata for providing access to its collections. The photographs are by S.W. Woo.

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Book Reviews

LEPIDOPTERAN ANATOMY. Eaton, J. L. 1988. 257 pp. Wiley-Interscience, New York ISBN 0-471-05862-9. $49.95.

This is yet another overpriced lousy book. To make matters worse, it is misleadingly titled: the title should be *The Anatomy of* Manduca sexta, because that is the only species illustrated. The book is mainly a collection and republication of Eaton's work on that species, which is of course very important in physiological and toxicological studies. Perhaps there will be follow-ups on other very important species, such as *Pieris brassicae*, *Galleria*, or *Bombyx mori* — but what can they be called if this book has co-opted the name of the entire order?

The illustrations are usable but remarkably crude. Many of them resemble casual preliminary sketches rather than publishable, definitive illustrations. Not unsurprisingly, they suffer from occasional errors which will not trouble most users but could lead graduate students, for example, astray. The most egregious of these are identified by neurobiologist Nicholas J. Strausfeld in his review of the book in *Quarterly Review of Biology 64*: 206–207, which should be pasted into every copy at large. The book also suffers from sloppy editing, many typos, no glossary (and many terms are quite unfamiliar, even to those with a passing knowledge of insect morphology), and a form of organization which makes the book needlessly difficult to use as a reference.

There is no attempt to place *Manduca* in any kind of ecological or phylogenetic context. This is inexcusable, especially since most of the really exciting work on Lepidopteran anatomy is being done in exactly that context, particularly by Niels Kristensen. Fortunately, Kristensen is heading up a synthetic two-volume work on Lepidoptera as part of the *Handbuch der Zoologie* which will, once it appears, become *the* standard (we are assured it will be published in English) and relegate this work to deserved obscurity. It will, however, be "institutionally priced" beyond any shadow of a doubt.

Study of the neuromuscular anatomy has the potential to provide a plethora of new and important taxonomic characters for phylogenetic reconstruction, if we can convince Lepidopterists to pickle specimens and then cut 'em up. This book could have had a valuable role in encouraging such developments, had its author and publisher taken a broader view. Instead, it is basically a "how-to-cut-up-a-*Manduca*" manual and might be useful for insect morphology courses in places where that beast is a pest and readily available. Publishers who issue misleading blurbs for new books, like the one put out by Wiley for this, deserve worse than contempt. They deserve to be boycotted.

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BIOGEOGRAPHY AND QUATERNARY HISTORY IN TROPICAL LATIN AMERICA. T. C. Whitmore and G. T. Prance (Eds.). Oxford University Press, Oxford. 214 pp. ISBN 0-19-854546-0. Price £45.00 (hardback).

During the early 1970s, many scientists working on the biogeography of Neotropical organisms, fell under the spell of what was to be called afterwards the "Pleistocene Refuge Theory". The simplicity and elegance of the evolution-

ary model, first proposed for South America by Haffer, and Vanzolini & Williams, rapidly gained many adepts. Unfortunately, a number of workers were misled by the oversimplification and popularization of the model, and applied it indiscriminately to several groups of organisms for which a poor or weak database was available. It is not suprising then, that by the end of the decade, several scientists were questioning strongly the model, pointing out its inconsistencies, and proposing alternative views.

The book under review has had a very long gestation period. I have been privileged to be allowed examination of preliminary drafts of portions of it, and have been witness to its development. I am under the impression that its publication would have had more impact a few years ago, as the subject is now considered somewhat *démodé*, having been incorporated uncritically into several textbooks.

Nevertheless, the different chapters included, are the best introduction available at present, on this fascinating interpretation of the biogeography of tropical South America which, as indicated in the Introduction, states: "...there are in the lowlands of tropical South America centres rich in species or characters separated by regions with a poorer or more mixed fauna. These centres were interpreted to coincide with refugia to which the rain forest was restricted at past times of drier, more seasonal climate."

The book is divided into seven chapters by four authors; their quality is uneven, but this should not be interpreted as implying that some authors are less knowledgeable than others. In fact, all four authors are respected authorities, with foremost experience of their specialities. Rather, the unevenness is a reflection of the widely differing amounts (and quality) of information available for the groups analysed (plants, by Prance; butterflies, by Brown; birds, by Haffer; and early man, by Meggers). It is immediately obvious that the paucity of data afflicts severely the contributions by Prance and Meggers; much finer analyses can be made with the wealth of information gathered for birds and butterflies. But even such a rich database has its interpretation problems; how can the superspecies-allospecies nomenclature of the ornithologists be reconciled with the more "orthodox" species-subspecies nomenclature of the lepidopterists? Haffer goes even as far as to recognize "first-order superspecies" and "second-order superspecies" (= megasuperspecies), while at the same time rejecting the "unqualified" use of subspecies, which he regards as possibly based on varying subjective criteria.

It appears to me that many of the "allospecies" recognized by ornithologists, are based on negative evidence ("absence or near-absence of phenotypic indications for hybridization in the populations along the contact zone"), while recognition of subspecies among butterflies is effected more as an extrapolation from a few observations made on contiguous natural populations hybridizing freely along narrow or very narrow contact zones (e.g. among *Heliconius*).

It should be understood then, that what ornithologists call "species" (or allospecies) does not mean necessarily the same for the lepidopterists; actually, there is a complete continuum between the case of two fully developed, closely related (sister) "species", completely sympatric, which never hybridize, and that of two sets of distinguishable (by whatever means, morphological, statistical, biochemical, caryological, etc.) parapatric populations, connected by a broad intergradation ("hybridization") zone. It is easy to recognize the former as an instance of two evolutionarily independent "species", but what shall (or could) the latter sets be named? One may decide to call them subspecies, and

that might be an appropriate and useful action, but where does the limit lie then between "species" and "subspecies"? At what hybridization rate do you stop calling them "species" and start recognizing them as "subspecies"?

This problem could be circumvented by using a "phylogenetic species" (e.g. diagnosed by unique combinations of characters) concept, instead of the more traditional "biological species" concept, in order to be able to prepare phylogenetic analyses of taxa. These in turn would be compared to area cladograms, searching for congruences, following the rules of vicariance biogeography. This approach has recently been applied by Cracraft & Prum (1988. Patterns and processes of diversification: Speciation and historical congruence in some Neotropical birds. *Evolution* 42: 603-620), obtaining some thought-provoking preliminary conclusions.

The above considerations may seem somewhat out of place in this review, but I believe they are fundamental to the main conclusions of this book: There are centres of endemism for groups of organisms in the humid tropical lowlands of Central and South America (although statisticians may frown about the methods employed in delimiting them), and they seem to require more than just an ecological explanation.

What is particularly worrisome, is that most recent criticisms directed against the "refuge theory," focus principally on the early data and preliminary hypotheses, presented in the first discussions on the subject, without taking into account the great deal of information gathered after the symposium at Macuto in 1979 (papers presented at that meeting were edited by Prance, 1982, *Biological Diversification in the Tropics*. New York, Columbia Univ. Press). For instance, two commonplace (and erroneous) generalizations, often attacked by the opponents of the "refugialists" are, first, that large portions of the humid tropical forest were replaced by savanna during glacial times and, second, that endemism centers are areas of maximal species diversity.

As regards the first argument, it has been shown that there are several more kinds of forest types than previously imagined, each with its own retinue of more or less specialized residents. It can be understood then that some organisms may dwell only in certain forest types, while others might be more tolerant. Thus, it is not necessary to invoke large-scale replacement of "forest" by "savanna" to produce vicariances in the distributions of highly specialized organisms: it might be enough to substitute for example a humid forest for a drier kind of forest to produce isolation of populations. This would explain why certain groups of (ecologically specialized) organisms are split into many more endemism centers than other (generalized) groups.

Another myth which must be abandoned (and this might produce some discomfort among conservationists who have used the refuge theory to propose areas for preservation of genetical resources), is that core areas represent centers of highest diversity; instead, diversity is maximal in transition areas *between* centers of endemism, where natural disturbances (by wind, fire, river dynamics, etc.) appear to be strongest.

This book must be read carefully by everyone interested in the subject; it is by far the most complete and authoritative treatment on the controversial ideas surrounding modern thoughts on the biogeography of tropical America, although obviously favoring a model of allopatric differentiation.

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THE ECOLOGY AND CONSERAVATION OF THE PURPLE EMPEROR BUTTERFLY (*Apatura iris*).
K. J. Willmott. 1987. Published by the author, London. 140 + 8 + 6 + 18 + 18 pp., ill., 3 pull out maps. Price not stated.

The publication under review is a report on a research project carried out in England by the author over three consecutive years (1981–1984) and taking into account his previous experience with the species. The publication was produced in a small number of copies. As it contains confidential information on localities and their owners, it is not offered for sale in a general way. The research and publication of the report were sponsored by "Associated Tyre Specialists" of Harrow (Middlesex). The author is not a professional entomologist, but has had some 20 years of lepidopterological experience when he started on the project. Topics from the contents include: Status and distribution; ecology of adults; Territories; Pairing; Ovipositing; Larval ecology instar by instar; The pupa; Behaviour; Conservation; The ideal habitat; Effect of Climate; Habitat management. The whole work is richly illustrated by photographs, line drawings and maps. The research has been carried out in the field and the danger of substituting captive breeding for extensive field work is pointed out. Some of the reasons for the fluctuation of *A. iris* populations are demonstrated including climatic effects during critical stages of the species' life-cycle. I would have wished to find more information on the methods and techniques used, on the population size, structure and dynamics (a very difficult task indeed with this species!) as well as a comparison between the assumptions of previous authors and the results of the present research. This is a minor criticism, outweighted by the excellent line drawings showing various aspects of the *A. iris'* ideal habitat, detailed maps of selected habitats, and diagrams warning of possible forms of habitat destruction and the instructive photographs. All in all, this is one of the best applied ecological studies for conservation purposes of a single butterfly species. It is to be hoped that the author will be given the opportunity both to continue his study of *A. iris* on a long-term basis as well as to expand his research in other areas and species; why not give him an opportunity to study all three European *Apatura* species on the Continent? On the work he has accomplished he fully deserves our compliments.

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TAGFALTER 2. Hans-Josef Weidemann. 1988. Neumann-Neudamm Verlag, Melsungen (Germany). 372 pp., col. ill.; ISBN 3-7888-0509-9. Price 48, — DM hardback.

This small pocket book is the conclusion of the book reviewed in J. Res. Lepid. **26**:288. Generally speaking, almost everything said in that review is relevant also to this volume. It deals with the "remainder" of the Lycaenidae and the families of Riodinidae, Nymphalidae, Satyridae and Hesperiidae, as recognized by the author. It is introduced by a general part dealing with butterfly biology including the early stages, butterfly conservation (the counterproductiveness of typical German contemporary alibi-legislation forbidding the collecting of

and research on nearly all European butterflies without a special permit given from case to case at the will of bureaucrats lacking knowledge of the problems is pointed out), key to larvae and a table of biological data. The systematic part is arranged in the same way as in the first volume; the word "Verhalten" (i.e. behaviour) is also missapplied in this volume to the time of appearance, voltinism and occasionally other aspects of adult biology and very rarely used in its correct sense. A systematic list of taxa with, in Weidemann's opinion, valid names and some synonyms as well as German vernacular names (often new), a bibliography and an index conclude the book. Some chapters were written chiefly by the Dutch butterfly ecologist F.A. Bink. The small size of about 11 × 18 cm is not to be recommended for this type of book. The book is richly illustrated by colour photographs, mostly taken by the author in captivity. Of 87 references cited by Weidemann 25 (30%) refer to his own papers, whereas numerous standard works are missing.

As in the case of the first volume, the most important parts of this book are interesting (representative?) observations on the biology of many species, whereas the systematic and related parts are much less worthy of attention. Unfortunately, the biological observations mostly lack information on the methods and techniques used to obtain them. Like in the first volume, the author split butterflies into two categories, K-strategists and r-strategists without ever having counted their populations, necessary information for making such judgement, assuming that there really are K-strategists among the butterflies (we know that all butterfly species are r-strategists!). Further, in the table of biological data, information is presented as fact without a statement as to how it has been obtained. Curiously, some of these "data" are quantified, like the egg load of all species, stated in numbers. As Weidemann's book is said to deal with the butterflies of Germany (the Alps excepted), I wonder why some Mediterranean (s.l.) species (in vol. 1 *Archon apollinus*, *Papilio hospiton*, *P. alexanor* etc.) have been included and *Erebia euryale* has been excluded. Most regretable is the misidentification of the figures of some species: the butterfly on p. 295 (top) is *Coenonympha tullia* (not *C. glycerion*) and of the six species figured on p. 307 only *Pyrgus malvae* and *P. cirsii* are correctly identified. Weidemann's comments on zoological nomenclature and the instability of scientific names are deplorable and naive. His remedy, the utilisation of "stable" German vernacular names, contradicts his changing probably a half of them around or replacing them by new original creations of his own. Like the first volume, this one is also full of statements that could be arrived at only after years of painstaking research. The study of distribution and population dynamics of *Carcharodus alceae* (cf. p. 324) would be methodically very difficult, if at all possible. The majority of Weidemann's readers will be amateurs unlikely to recognize these shortcomings, which makes them even more dangerous. I cannot explain Weidemann's obsession of enclosing many terms in inverted commas; I suspect his uncertainty in matters of terminology is the reason of this bad form.

It is difficult to pass a definitive judgement upon this book, praised by many reviewers. On the one hand it is far more than the simple small pocket book it really is, and should probably deserve much praise as such, had it been better written. On the other hand, it must be judged as a serious attempt at a natural history of German butterflies, and as such it leaves much to be desired. I would prefer to judge it just as a first draft of a manuscript presented for discussion

before being finalized. I would surely congratulate its author under such circumstances.

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LISTE INVENTAIRE SYSTEMATIQUE ET SYNONYMIQUE DES LEPIDOPTERES DE CORSE. Charles E. E. Rungs. 1988. Alexanor (Suppl.) **15**:[1]–[86]. ISBN 2-903273-02-2. Price not stated.

The publication under review is a supplement to the popular Leraut's catalogue of the Lepidoptera of France and Belgium and deals with all families, including the "Microlepidoptera", listing a total of 1386 species. The species are listed in systematic order, some with the usual synonyms added to the valid name. Apart from the systematic list of taxa, there are an extensive bibliography (around 400 titles); explanatory notes and comments on the taxonomy, nomenclature, occurrence in Corsica and other aspects concerning 77 taxa; an index of abbreviations of author's names; an alphabetic index of scientific names and an appendix listing species to be excluded from the fauna of Corsica mostly for being misidentified by previous authors. Species entries are numbered; each entry includes the author's name in full and the year of publication, as well as the relevant subspecies or "subspecies" name. All entries are cross-referenced to Leraut's catalogue and some to the numbered annotations at the end of the systematic part.

Rungs is not quite as generous as Leraut in his recognition of generic status of some of at best subgeneric names (e.g. he does not recognize Leraut's "genus" *Lysandra*), but he certainly is a splitter in my view, having recognized weak "genera" like *Heodes, Fabriciana* and *Cynthia*. He is certainly very generous in attributing the rank of subspecies to some unequivocally infrasubspecific names: *Anthocharis cardamines cardamines meridionalis* (Verity, 1908), originally proposed for an infrasubspecific race from Florence is treated as a Corsican subspecies of this species, and Verity's seasonal form *calidogenita* described from Italy: *Toscana* is treated as the valid name for the Corsican subspecies of *Celastrina argiolus* (Linnaeus, 1758). As Rungs correctly listed all authors' names in full, I fail to follow why he published the list of their abbreviations. The omission of parenthesis for the names of authors of species-group taxa listed in combination with a generic name other than that forming the original combination can be accepted in a faunistic and similar publication; it is regretable in a systematic catalogue like this. It would have been better to place the page numbers in parenthesis, to distinguish them from unbracketed pages of the same volume, than to employ for the purpose square brackets which have a different specific purpose in taxonomic publications. In spite of these criticisms, I am sure that the publication under review can be of interest to any serious student of the Lepidoptera of Corsica.

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LEPIDOPTERA. II. Rhopalocera, Hesperiidae, Bombyces, Sphinges, Noctuidae, Geometridae. W. Mack. 1985. In: H. Franz: DIE NORDOST-ALPEN IM SPIEGEL IHRER LANDTIERWELT. Band V. 484 pp.; Universitätsverlag Wagner, Innsbruck (Austria). Price cca 240, — DM. (In German).

The first part of the fifth volume of the monumental monograph of the northeastern (Austrian) Alps was devoted to the "Microlepidoptera"; the second part, here under review, is fully devoted to the "Macrolepidoptera". It deals with the Rhopalocera (incl. superfamilies Papilionoidea and Hesperioidea) and Heterocera (the "Bombyces", "Sphinges", Noctuoidea and Geometroidea). The author of this book, who died before the manuscript went to press, was little known outside his own "home range"; he spent most of his life as a natural science teacher at a grammar school ("Gymnasium") in Gmunden, lepidopterology being his lifelong hobby, although he was a naturalist by education. The book under review is little known by European lepidopterists, but constitutes one of the most painstaking compilations of faunistic data I have ever seen. Apart from general information on the range, ecology and other aspects, it lists all records of the species from the area studied, divided into 11 smaller districts. Each record provides information so far as is known on the collector or author, locality, date, method of capture, altitude and source of reference. The large-size (A4) book is concluded by an extensive bibliography and an alphabetical index to scientific names. It is difficult to review a book of this type. It is a "boring" and expensive book lacking illustrations, practically an enormous collection of records, as they are seldom found. I would wish to have someone take up the records collected on the about 190 butterfly species recorded in the northeastern Alps, as contained in this book, bring them up to date, analyze them and utilize them for the conservation of the rich butterfly fauna of the area. I recommend the book to anyone interested in the Lepidoptera of Austria and the Alps; it is well worth paying the high price the publishers ask for it.

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DECLINE AND CONSERVATION OF BUTTERFLIES IN JAPAN I. Hama, E., M. Ishii, & A. Sibitani. 1989. Lepidopterological Society of Japan, Osaka. 145 pages + x, 14 color plates. 1500 Yen. In Japanese, English summaries

Although the Japanese as a nation are widely viewed as unrestrained environmental despoilers, this fine volume indicates there is a sensitive cadre of individuals with great concern to what is happening to their homeland. A series of papers herein show the conservation situation in Japan is strikingly similar to that in most other industrialized nations, with butterflies, as key indicators of ecosystem fitness, declining under many circumstances.

The three editors combined the efforts of 19 contributors to round out the volume. It is organized as a series of case histories of 22 butterfly species which together are found across a wide variety of habitat types of the peninsula. Each case gives the details for that species in a specific area for which long term (at

least ten years) information are available, including facts relating to the species decline or extirpation. All families are covered, and most species are local sedentary animals. Unfortunately, these accounts are in Japanese so the information was only accessible to me from the brief English summary of each. The tables, maps, and photographs accompanying each account imply the treatments are descriptively thorough, but frustrating for an English limited person.

A 7 page introductory essay by Sibatani gives an outstanding overview of the conservation status of the butterfly fauna of the country. The first legislation to protect butterflies dates from the mid-1930's, when special populations at specific sites were designated *Tennen Kinenbutu* or "natural monument things". The protection was in the form of collecting prohibition. The trend of protection continues to the present, with 37 species now "monuments". As is well known, this action has almost no effect in bringing about the advertised protection. Thus Japan repeats the German fallacy. Sibatani gives a tabular summary of the 22 treated species with years of extinction or decline, year of protective action, and processes and possible causes of decline cited.

The Environmental Agency of Japan is making a survey of the biota of the county, but no results are yet in. Clearly there is growing awareness of conservation issues. We must applaud the Lepidopterological Society of Japan for taking a leadership role in calling attention to the plight of the rich endemic biota of its area of expertise. This is an historically important position paper. We strongly encourage joint exchanges of information and moral support to the movement to conserve what we can of the natural world. We are applying to the Society to permit us to reprint Prof. Sibatani's paper in order that a wide audience of non-Japanese language workers can share in this distressing situation.

R. H. T. Mattoni, 9620 Heather Road, Beverly Hills, CA 90210 USA

INSTRUCTIONS TO AUTHORS

Manuscript Format: Two copies *must* be submitted (xeroxed or carbon papered), double-spaced, typed, with wide margins. Number all pages consecutively and put author's name at top right corner of each page. Underline all words where italics are intended. Footnotes, although discouraged, must be typed on a separate sheet. Do not hyphenate words at the right margin. All **measurements** must be metric. Metric altitudes and distances should include imperial equivalents in parenthesis. **Time** must be cited on a 24-hour basis, standard time. Abbreviations must follow common usage. **Dates** should be cited as example: 4. IV. 1979 (day-arabic numeral; month-Roman numeral; year-arabic numeral). Numerals must be used before measurements (5mm) or otherwise up to number ten e.g. (nine butterflies, 12 moths).

Title Page: All papers must have the title, author's name, author's address, and any titular reference and institutional approval reference, all on a separate title page. A **family citation must** be given in parenthesis (Lepidoptera: Hesperiidae) for referencing.

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The Zoogeography and Systematics of the Argentine Andean and Patagonian Pierid Fauna

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Abstract. The geographic distributions and systematics of the Pieridae of the Andean highlands and Patagonia, Argentine Republic, are reviewed. Previously unpublished records based on twelve years' field work by the author and collections in Argentina, the United States, the United Kingdom, etc. are provided to clarify zoogeographic and systematic problems in this fauna. *Tatochila blanchardii* is reduced to a subspecies of *T. autodice*. The taxa *T. arctodice*, *macrodice*, *sterodice*, *vanvolxemii* and *fueguensis* all become subspecies of the widespread polytypic species *T. mercedis*. The possibility that *Hypsochila wagenknechti* and *H. galactodice* are conspecific is discussed. Records of putative *galactodice* from the *puna* of Jujuy are presented. The taxonomic history of *Phulia nymphula* in Argentina is clarified, and its range extended south to western Neuquén. Precise localities are given for the first time for the Chilean taxa *Eroessa chiliensis* and *Mathania leucothea* in Argentine Patagonia. *Colias flaveola* is reported for the first time in Argentina. *Colias mendozina*, rediscovered in the highlands of Mendoza, is treated as a full species. Zoogeographic relations among the *puna*, the pampean ranges (Cumbres Calchaquíes — Sierra de Aconquija), the main *cordillera*, the Cordón del Viento, and Patagonia are clarified by the Pierid data. Previous work has overemphasized the distinctness of the Fuegian fauna, whose only important Pierid endemic is the possibly-extinct *Colias ponteni*.

Subspeciation in most genera is probably of Quaternary origin, but speciation and certainly the origin of endemic genera or species-groups antedates the Pleistocene. The existing Pierid fauna represents the current stage in a long and complex process involving dispersal, vicariance, and evolution, the outlines of which are only beginning to emerge. Current distributions reflect both contemporary ecological phenomena and the long-term sequelae of past faunal movements in response to geoclimatic change.

Resumen. La fauna de mariposas Pieridae de los sectores altoandinos y patagónico-fueguinos de la República Argentina fue analizada del punto de vista zoogeográfico — histórico, utilizando muestreos basados en 12 años de colecta por el autor y los registros confiables de diversos museos y colecciones en dicho país, Estados Unidos y Inglaterra, entre otros. La *Tatochila blanchardii* por razones de intergradación espontánea ya se halla subespecie de *T. autodice*. Las taxa *T. arctodice*, *macrodice*, *sterodice*, *vanvolxemii* y *fueguensis* cambian en subespecies de la especie politípica muy ampliamente difundida *T. mercedis*. La ocurrencia de fenotipos muy parecidos a la *Hypsochila*

galactodice en la puna argentina indica la posibilidad de simpatría con la *H. wagenknechti sulfurodice* en dicha zona, a pesar de la ambiguëdad de la relación de estas "especies" mas al sur. Se aclara la historia muy confusa de la taxonomía del genero *Phulia* en el Cono Sur, y se presenta registros mas australes que los anteriormente conocidos. También se ofrece registros minuciosos de las mariposas chilenas *Eroessa chiliensis y Mathania leucothea* en la Patagonia argentina y de *Colias flaveola* en la cordillera de San Juan por primera vez. La *Colias mendozina*, recien descubierta en la cordillera de Mendoza, se coloca como especie. Se aclaran las relaciones entre la puna, las Sierras Pampeanas, la cordillera, el Cordon del Viento, la Patagonia y la Tierra del Fuego, mostrando entre cosas una enfasis no justificada en el tratamiento de la pieridofauna fueguina, cuya unica especie endemica es la *Colias ponteni*, "perdida" desde 1852.

Para explicar los patrones de especiacion y distribución de dicha fauna hay que desarrollar un esquema historico tomando en cuenta los cambios geofisicos y climaticos del continente y vinculando los ambientes tropicales con los extratropicales y los altos con los bajos. Segun parece la especiacion y seguramente el origen de generos y subgeneros o grupos de especies ha sido anterior a la Pleistocena, aunque la subespeciación, como en la *T. mercedis*, sea fenomeno pleistoceno y/o holoceno. El estado actual de la fauna refleja una historia muy complicada de dispersion y migracion, mezclada con procesos de vicariancia tal que no se puede atribuir todo a ningún solo proceso evolutivo y/o faunístico.

El cuadro que doy al final de este articulo, sin contener casi nada de nuevo, excepto quiza algunos datos biologicos de poca importancia, tiene por objeto mostrar de un solo golpe de vista ese laberinto en parte desembrollado...demostrar que desgraciadamente nuestros conocimientos sobre las especies del género *Tatochila* son aún muy incompletos....Surge inmediatamente la vieja cuestión: ¿son especies o son variedades? Sabido es que este término *especie* es por demás elástico...[1]

Eugenio Giacomelli, 1915

Introduction

Twenty years ago the lowland tropics were commonly viewed by biologists as a sort of museum of living fossils, persisting untouched through the ages while the biota of higher latitudes was decimated and reinvigorated by the geoclimatic catastrophes of the Quaternary. Academic discussions of the causes of tropical biotic diversity — which

[1] "The chart which I give at the end of this article, without containing anything much that is new except a few biological data of little importance, has as its object to demonstrate at a glance this partly-disentangled labyrinth...to demonstrate that, unfortunately, our knowledge of the species of the genus *Tatochila* is yet very incomplete...The old question immediately arises: are they species or varieties? It is known that this term *species* is, moreover, elastic..."

typically meant tropical lowland rainforest biotic diversity — were very popular in the 1960s. In this context, the "geologic time hypothesis" claimed that a vast flow of time uninterrupted by disaster had allowed biotic richness to accumulate unencumbered in low latitudes. That view was later stood precisely on its head. By the 1980s the "refugial hypothesis" had become the conventional wisdom: the tropical forest had been fragmented repeatedly in the Quaternary, dividing populations and promoting speciation. Instead of stasis, the tropics were now seen to be in a state of perpetual dynamism; instead of antiquity, species were now seen as manifestations of the recent past — an equally erroneous view, as subsequent events have shown.

The locations of proposed Quaternary refugia in the tropical lowlands are inferred from contemporary biological phenomena, such as the geographic distribution of endemism and of zones of intergradation or hybridization (the two are not necessarily the same). Extremely little paleoclimatic information is available for the lowland tropics, primarily because suitable depositional environments for pollen and other fossils are rare (cf. Liu and Colinvaux 1985, 1988). To a degree which can be embarrassing to some of its practitioners, the refugial theory is pegged to climatic reconstructions in the Andean highlands (where excellent palynological records abound) (Shapiro 1989a). At present there are no satisfactory dynamic climate models incorporating orographic effects which relate the highlands to the tropical forests, permitting a test of refugial scenarios derived from present distributions. Progress is being made in refining the existing crude models (Manabe and Hahn 1977, Rind and Peteet 1985), but until they are much better this will remain an important structural weakness of refugia as a purported synthetic theory.

The asymmetry in paleoclimatology is mirrored in biogeography: there have been few in-depth studies of highland organisms, and our knowledge of their distribution is proportionately poorer than in the lowlands. Published distribution maps create a false impression of good coverage. On closer inspection one typically finds the dots are distributed along the major trans-Andean highways. One of the first efforts to correlate animal speciation and distribution in the Andes with Quaternary climatic dynamism was by Adams (1973, 1977) and Adams and Bernard (1977, 1979, 1981), working on the pronophiline Satyrid butterflies of the Colombian and Venezuelan Andes and nearby ranges. But Adams merely suggested a mechanism for speciation — a plausible and quite conventional one — and was unable to correlate specific species with specific geohistorical events, since most of the relevant palynology had not been published yet. Indeed, there is nothing in Adams' work which enables us to differentiate between geoclimatic dynamism and contemporary ecological forces to account for the pattern of narrow altitudinal ranges and serial species replacement along transects which is characteristic not only of Pronophilini but of tropical organisms generally (Stevens 1989). A decade has

passed, but little progress has been made; most of what is being said about high-Andean organisms remains at the arm-waving stage. Nonetheless, the importance of the problem of high-altitude tropical biogeography has been recognized. It has even led to the publication of not one but two attempts at synthesis, however premature (Whitmore and Prance 1987, Vuilleumier and Monasterio 1986).

Basically we are asking whether it is possible to find an unmistakeable footprint of the Quaternary in the geography of the high-altitude biota, when we have paleoclimatic reconstructions from the immediate neighborhood. If not, the prospects of validating lowland scenarios with highland paleoclimatology look especially bleak. But we are also asking whence comes the highland biota and how old it is. This is a different and largely independent set of questions, because taxonomically the high-Andean biota has remarkably little connection with the tropical lowlands nearby.[2] Indeed, the taxonomic decoupling of high and low altitudes in the Neotropics is such a striking phenomenon that it seems as if it *must* bear on the geologic evolution of the region and have important implications for how we look at the problem of diversity — even if no one has any idea what they might be. Chabot and Billings (1972) addressed the question of how high-altitude floras originate, using the geologically young and relatively isolated Sierra Nevada of California as their example. They found a small floristic contribution from circumpolar-boreal sources. The principal source was the adjacent Great Basin, and they were able to identify physiological adaptations to the Great Basin climates which preadapted species to enter the alpine as it appeared. But the principal geographic sources of the high-Andean biota are in many cases not in adjacent climates but in another hemisphere, raising special and very interesting problems (Van der Hammen and Cleef 1987, p. 159). Raven and Axelrod (1974) attempted to assess probable antiquity of the various Andean plant families (and make Crucifers, hosts of most Pierini, quite late — late Miocene-Pliocene — though Tropaeolaceae were clearly there earlier and probably evolved there).

Among the Andean butterflies the Pierids have distinct advantages for biogeographic study. Their diversity is great enough to be interesting and quantifiable, but not so great as to be overwhelming. (Ulti-

[2] Descimon, 1986, p. 526 states categorically that "...it is clear that the Neotropical and southern temperate regions contributed little (or nothing) to the oreal butterfly fauna of the Andes. Its affinities lie instead with the Holarctic realm." The dangers in such generalizations have been demonstrated in recent revisionary work on the Argentine Theclini by Kurt Johnson and his coworkers. Johnson finds that the "Andean *Incisalia*" (*Thecla culminicola* group) are "a sister-group of the diverse and primarily montane Neotropical...groups...not an immediate southern relative of cryptically-marked Nearctic *Incisalia*" (Johnson *in litt.*, 7 April 1989). As a cautionary note I mention that *Tatochila* and the Neotropical genus *Ascia* show striking electrophoretic similarities, as well as resemblances in anatomy of the early stages (Shapiro and Geiger, unpublished). If this relationship is real, however, the direction of evolution has not been established.

mately the Andean Theclines, with their high diversity, may be the most informative butterfly group. However even their generic-level taxonomy remains fluid, many taxa are undescribed, and distributional data are fragmentary at best.) The Pierids are medium-sized, conspicuous, often easily reared, and not prone to cryptic speciation. They are the most conspicuous element of most high-Andean butterfly faunas: most of the common, widespread species are Pierids (and they were commented upon by many early travelers, such as Whymper (1892)). Their colors and patterns, as noted by Descimon (1986), are comfortably familiar to biologists of Holarctic origin, the product either of common ancestry or striking convergence — as usual, posing the problem of telling the difference. Most of these factors were noted by the end of the last century. Unsatisfactory as it is, it is not accidental that the Andean Pierid literature is better (richer) than that of any other high-Andean butterfly group. Descimon (1986) emphasizes the Pierids for all these reasons when he attempts a synthesis of high-Andean butterfly biogeography.

Another ongoing problem of refugial theory has been its failure to integrate its scenarios for both climate and biogeography in northern South America with the large, powerful and growing body of paleoclimatic evidence from farther south. Among the best-studied regions on earth from a palynological-paleoclimatic standpoint are Patagonia and Fuegia. Moreover, some of the information emerging from them is strongly at variance with the currently conventional wisdom on the geohistory of the continent, particularly the timing of the most important uplift (Clapperton 1983, Mercer and Sutter 1981). The Patagonian and Fuegian butterfly faunas are taxonomically unbalanced (dominated by Satyrids) but not especially impoverished. They are instructive in their apparently very close ties to the faunas of the high central Andes and also in the character and level of their endemisms. They are highly relevant to the interpretation of the Andean faunas as a whole.

The group of endemic pierine genera including *Tatochila* and *Phulia* has been monographed by Field (1958), Herrera and Field (1959), Field and Herrera (1977) and Ackery (1975). This body of work has made the Andean pierines attractive for biogeographic interpretation, as by Brown (1987) and Descimon (1986). But if the data for Pierini are, relatively, unusually good, they are still not very good in the absolute sense. It is possible to extract meaningful inferences from fragmentary data, and perhaps even to arrive at correct scenarios based on them. But one should not count on it Even for Pierids, almost every field trip to the high Andes or Patagonia turns up important surprises; for Lycaenidae or Hesperiidae, such surprises are guaranteed.

This paper draws on both published and unpublished data in an attempt to pull together and analyze the zoogeography and systematics of the Andean and Patagonian Pierid fauna of the Argentine Republic. It calls on field trips undertaken over 12 years, comprising over 18,000 miles of travel on the ground, from the Bolivian border to

Ushuaia, Tierra del Fuego — as well as on the accumulated experience of previous butterfly workers in that country. Argentina comprises an array of biomes ranging from tropical rain forest to cold steppe and periglacial tundra. Northwest Argentina is at the margin of the great Andean *altiplano*, the center of diversity for the miniature Pierids of the *Phulia* lineage, and of the dissected *jalca* or "*páramo*" where *Tatochila* achieves its greatest diversity. The *altiplano* is manifested in the *puna* of Salta and Jujuy and the highest elevations of the *Sierras Pampeanas*, while the "*páramo*" can be seen in, for example, the Cuesta del Obispo and the mid-reaches of the *Sierras Pampeanas*. If Pierid diversity does not quite match Arequipa or Cusco, it is still sufficient to be informative. More importantly, the geography is singularly favorable for tracing the rarefaction of northern (i.e., tropical) lineages as one proceeds southward into temperate climates, and *vice versa*. In so doing, one connects Patagonia and Fuegia to the central Andes at last, within the taxonomic limits set below.

Of the Andean countries, Argentina may not be the most critical in terms of its overall potential contribution to historical biogeography, but it is certainly not the least and it is definitely the easiest. Working out Argentine Pierid faunistics is logistically feasible. Doing the same for Peru or Bolivia, which may have more to say about coupling the highlands and the lowland tropics, is a much more daunting project (barely begun for Peru by Lamas, 1982): the faunas are much richer, there is much less of a data base, and field work is much more difficult. Repeating the task attempted here for Argentina for other countries and other taxa will be a slow, agonizing process, but there is no substitute for it. Perhaps the next attempt at a synthesis of high-altitude tropical biogeography will be shorter on speculation and much longer on hard data where the butterflies are concerned. Perhaps some day there will even be an integrated overview of continental paleoclimates and paleobiogeography for South America, and the butterflies will be a significant group in its preparation.

Defining the Target Fauna

Breyer (1939) provided the first systematic list of Pieridae from the entire Argentine Republic. It reveals a large Neotropical, lowland — lower montane element distributed in the Northeast, the Chaco and the Yungas. Because the affinities of this fauna, as well as its south- and westward limits, are so clear, I have not treated it in this paper. A study like Larsen's (1984) for the Arabian Peninsula, which seeks to identify the relative contributions of different source regions to a "crossroads" fauna, is particularly interested in such things as the tropical-temperate transition alluded to here. But the taxa of *Phoebis*, *Eurema*, *Zerene*, *Anteos*, *Leptophobia*, *Perrhybris*, *Pereute*, *Appias*, *Catasticta*, *Hesperocharis*, *Dismorphia*, *Pseudopieris*. . . barely if at all impinge on the objectives of this paper. Of the group of long-range

migrants, *Eurema deva* Dbl. and *Colias lesbia* Fabr. have been included because they penetrate (and breed seasonally) so far into the middle latitudes, while *Phoebis sennae* L. and *Ascia monuste automate* Burm. have been excluded because they rarely penetrate south of Buenos Aires. *Theochila maenacte* Bdv. poses a unique problem. It does not appear in the analyses because it is confined to lowlands in the Northeast, south to greater Buenos Aires. But it is discussed in the text because of its close phylogenetic relationship to *Tatochila* and its broader biogeographic import. *Teriocolias* also poses a problem. It is a montane insect whose seasonal cycle includes regular up- and down-slope movements which make it a component of the highland fauna. On that basis it has been included in the analyses, and a few new data are reported (cf. Schaefer and Breyer 1941).

After all these somewhat arbitrary decisions, the fauna comprises: all the Argentine taxa of the genera *Phulia*, *Hypsochila*, *Tatochila*, *Eroessa*, *Colias* and *Teriocolias*, plus *Mathania leucothea* Mol. and *E. deva*. The concluding analysis incorporates Chilean data, adding a few taxa of the above genera plus *Infraphulia ilyodes* Ureta, *Pierphulia rosea* Ureta (two subspecies) and *P. isabela* Field and Herrera — any of which might still turn up in the poorly-collected *puna* of far NW Argentina.

Phytogeographical Analyses of Argentina: an Overview

Argentina has a venerable tradition of ecology and natural history and an extensive domestic literature in Spanish, which is largely unknown outside the country. There have been several comprehensive attempts to schematize the ecobiogeography of Argentina, one of which (Shannon 1927) actually emphasized entomological considerations. The majority, however, are concerned with climate and plant communities (taxonomically defined) or formations (physiognomically). In 1953(a) Cabrera summarized and attempted to synthesize these. He updated this work in 1971; what follows is largely abstracted from that paper (Fig. 2), but with some input from Castellanos and Pérez Moreau (1945), Sarmiento (1975), Hueck and Seibert (1972), Cabrera and Willink (1980), Davis (1986) and Irwin and Schlinger (1986) with additional from Gómez Molina and Little (1981) on mountainous regions and Correa Luna *et al.* (1977) for the National Parks. Figs. 3–5 are from Madsen *et al.*, 1980, redrawn and should be used in conjunction with Cabrera. Given the montane-austral focus of this paper, the lowland tropics and subtropics are not discussed below.

Cabrera divides Argentina into two regions, five domains, and 13 provinces, as follows; those marked * are discussed in more or less detail in this paper:

I. Neotropical Region
    A. Amazonian Domain
        1. Yungas Province*

2. Paraná Province

B. Chaco Domain

3. Chaco Province
4. Espinal Province
5. Prepuna Province*
6. Monte Province*
7. Pampa Province

C. Andean — Patagonian Domain

8. High-Andean Province*
9. Puna Province*
10. Patagonian Province*

II. Antarctic Region

A. Subantarctic Domain

1. Subantarctic Province*
2. Insular Province

B. Antarctic Domain

Many of the habitats described below are illustrated in Plates I–IV.

Yungas Province. The Yungas occupy a narrow altitudinal belt on the eastern slopes of the mountains lying in or just barely beyond the tropics in northern Argentina, from roughly 500 to 2500 m above sea level. They extend far N into Bolivia, and S only to the north of Catamarca in the Pampean Sierras (Sierra de Aconquija), but including all the ranges in Tucumán. The climate is warm and humid, with most of the rain falling in summer. Precipitation ranges locally from 700 to 2500 mm or more, with very pronounced orographic effects. Mean annual temperature also varies greatly: from 14 to 26°C. A great variety of microclimates thus exists. Winter frosts occasionally occur at lower elevations and are common higher, where heavy snow may fall several times a year. In the tropics there is no true winter, and any snow that falls at these altitudes does not persist.

The predominant vegetation is cloud forest, with trees reaching 30 m in height and abundant lianas, epiphytes, and a dense understory of herbs and shrubs. Various transitions from such vegetation to desert, steppe, shrub-steppe, and temperate deciduous forest occur; ecotones may be gradual or abrupt, the latter usually reflecting rain shadows or the altitudes of semi-permanent inversions. Some of the most dramatic vegetational transects in South America may be made here, particularly in Tucumán. Cabrera divides the Province into three Districts, viz.:

(a) *Transitional Forest.* This is the transition from Yungas to Chaco, occurring from Pocitos to Orán in northern Salta; on the E flanks of the Sierras Maíz Gordo, Centinela and Santa Bárbara, etc. in Jujuy, the valley of Lerma and the mountains of Metán and Rosario de la Frontera again in Salta, the lower slopes of the Sierra de Medina and the Aconquija-Calchaquíes ranges in Tucumán. Temperatures are

high but precipitation relatively low (700–1000 mm), and deciduous trees, especially rather small Leguminosae, predominate.

(b) *Mountain Forest.* This narrow belt occurs above the preceding, reaching up to 1300 to 1800 m. It is very rich floristically and faunistically and commonly includes the southernmost populations of many lowland-tropical organisms on the continent; this is the so-called *selva Tucumana*. Precipitation is from 1500–2500 mm or locally higher; temperatures within the forest are cool in the intense shade and, frequently, in cloud and mist. Characteristic of this forest is the *horco molle* tree, *Blepharocalyx gigantea*, but many other conspicuous tree species occur. Butterfly species richness here is similar to that observed in the warm, humid far NE of Argentina.

(c) *Mountain Woodland.* This is the uppermost stratum of the Yungas and marks the transition from Mountain Forest to the treeless formations of the high mountains. Some characteristic woody species are *Podocarpus parlatorei*, alder (*Alnus jorullensis* var. *spachii*), elderberry (*Sambucus peruviana*), *Schinus gracilipes*, etc. with local outliers of *quenoa* (*Polylepis australis*) generating a spotty second treeline above 2500 m in some locations (Fernández 1970). The woody flora includes both Holarctic and Subantarctic elements. The herbaceous flora is very rich and includes many showy wildflowers, largely of Holarctic origin. The higher meadows — as between Tafí del Valle and Abra Infiernillo — include many perennial bunchgrasses. Above 2000 m trees are often confined to creek bottoms. Meadow and brush vegetation may occur much lower, however, as on the Cumbre de San Javiér near San Miguel de Tucumán, and it is unclear whether this reflects the well-known "telescope effect" found in tropical mountains or the medium- to long-term consequences of land use. Similar vegetation occurs at the highest elevations of the Sierras of Córdoba, representing a far-southern outlier of the Yungas.

Prepuna Province. This is the vegetation of the dry slopes and canyons from Jujuy to La Rioja, mainly between 2000 and 3400 m, but locally down to 1000 m in certain microclimates. It intervenes between the uppermost Yungas and the true *Puna*, but also between the Chaco and the *Puna* or the Monte and the *Puna*. The climate is warm and dry, with rain exclusively in summer thunderstorms. The vegetation is xerophytic shrub-steppe with aspect dominance by columnar cacti, of which *Trichocereus pasacana* and *T. terscheckii* are typical in the N and S respectively. Terrestrial Bromeliads and shrubby Leguminosae abound. Common genera include *Adesmia*, *Azorella*, *Junellia*, *Mulinum*, *Nassauvia*, *Parastrephia* and *Senecio*. Riparian woodland occurs in canyon bottoms, with *molle* (*Schinus areira*) and *chilca* (*Baccharis salicifolia*). Because of its complex geography, *prepuna* has little distinctive butterfly fauna and indeed is often rather depauperate, though it occasionally serves as a corridor to bring higher-altitude species

lower and *vice versa*, in butterflies as in plants. A major reference is Hunziker (1952).

Monte Province. The *Monte* begins in the valley of the Río Santa María in the Valles Calchaquíes, extending S through the W of Tucumán and La Rioja, through Mendoza and San Juan and thence into Neuquén and the E of Río Negro and in dilute form even to far NE Chubut. Precipitation varies from 80–250 mm (locally higher), mean temperature from 13–17.5°C, with pronounced climatic gradients both E–W and N–S. The vegetation is desertic and diverse, but dominated throughout by creosote bush (*Larrea* spp.) and mesquite (*Prosopis* spp.) except in alkali sinks, where *Distichlis* and Chenopods predominate. Common genera include *Bougainvillea*, *Bulnesia*, *Caesalpinia*, *Cassia*, *Cercidium*, *Mimosa*, *Trichocereus* and *Zuccagnia* and in gullies *Acacia* and *Celtis*. The *Monte* corresponds ecologically to the Sonoran Desert of North America, and like it segues almost imperceptibly into adjacent colder formations. Large-scale comparisons of community organization and function were made between the *Monte* and the Sonoran Desert as part of the International Biological Programme and are summarized in Orians and Solbrig, 1977.

Pampa Province. This is the bunchgrass prairie ofArgentina, much of it now degraded and invaded by exotic weeds. It occurs at low to moderate elevation in flat to rolling country in the E, roughly between 31–39°S. There are pronounced climatic gradients, particularly in precipitation, from 1100 mm in the NE ("subhumid *pampa*") to 600 mm in the SW ("subarid *pampa*"). The various floristic subdivisions are unimportant for this paper. The butterfly fauna has surprisingly low endemism.

The Andean – Patagonian Domain: General Considerations. The following translation from Cabrera (1971, p. 29 ff.) captures the character of the Domain well: "In the Argentine Republic this Domain extends all along the extreme W of the country, covering the *puna* and the Andean *cordillera* from the border with Bolivia to the S of Mendoza. There it begins to reach out to the E on the mesetas and the Patagonian ranges, reaching the Atlantic in Chubut and Santa Cruz. Its climate is cold and dry, with frosts almost all year and snow in winter. The Andean-Patagonian Domain is characterized by the scarcity of endemic families (of plants), only the Malesherbaceae and Nolanaceae being exclusive to it, and in turn a great richness of endemic genera of the most diverse groups. The families of greatest importance for their richness in genera and species are the Composites, Grasses, Verbenaceae, Solanaceae, Cruciferae, etc. The Legumes are represented by few genera, principally Papilionaceous, but at times with numerous species, as in *Adesmia* and *Astragalus*. The Zygophyllaceae and Mimosoid Legumes, so abundant in the Chaco Domain, are almost completely lacking. The dominant vegetation is shrub- or herbaceous steppe, with

extreme forms of adaptation to wind and drought. . .Where springs exist or water accumulates, inundated meadows form, called *vegas* in the *cordillera* and *mallines* in Patagonia." Cabrera gives a detailed subdivision of the Domain.

High-Andean Province. Again from Cabrera 1971, p. 30: "From the border with Bolivia to Tierra del Fuego. In Jujuy and Salta found approximately above 4400 m; in Mendoza above 3000, in Neuquén and Río Negro above 1600 m and in Tierra del Fuego above 500 m. . . . Immature, rocky or sandy soils, with a high-montane climate, cold and dry (except in the S), with snow or hail at any time of year. The mean temperature is low, below 8°C (−1.5°C at Crísto Redentor, Mendoza, at 3829 m). The vegetation is very poor and is formed by grassy steppe or steppe of cushion chamaephytes. . ." Three Districts are recognized, which are very important for understanding the butterfly fauna:

Quichua District. This is the true high-Andean vegetation, occupying the Eastern, or Royal Cordillera S to the N of San Juan from 4300–5600 m. It is thus tropical and subtropical. Precipitation is higher in the N and E, where the District contacts the Yungas and Chaco, than in the S and W where it contacts the Monte. It is strongly seasonal, concentrated in afternoon thunderstorms during the "Bolivian Winter" from November to February caused by the S-ward migration of the Intertropical Convergence Zone in response to heating in the continental interior. The most common climax formations recognized by Cabrera are: *Festuca orthophylla* — *F. chrysophylla* — *Poa gymnantha* steppe, with such associated spp. as *Stipa* and *Deyeuxia*, *Baccharis incanum*, *Senecio graveolens*, *Werneria poposa*, *Adesmia caespitosa* and *patancana*, and the remarkable *yareta*, *Azorella compacta* (Umbelliferae), a cushion plant formed of thousands of tiny terminal rosettes; also smaller, delicate wildflowers including *Perezia ciliosa*, *Silene friesii*, *Cajophora coronata*, *Calceolaria glacialis*, *Valeriana spathulata*, *Nototriche anthemidifolia*, etc.; steppe of vizcacha grass (*Stipa frigida*) with shrubs such as *Artemisia copa* and *Senecio viridis*; Bitter Coirón (*Stipa chrysophylla*) — vizcacha grass steppe associated with the dwarf Leguminous shrubs *Adesmia glanduligera* and *A. nanolignea*; and others. Some additional characteristic or indicator species are: among the cushion plants, *Oxalis compacta*, *Senecio algens* and *Pycnophyllum molle*; very high-altitude Crucifers (*Aschersoniodoxa mandoniana*, *Parodiodoxa chionophylla*, both reaching above 5000 m); sedges of inundated *vegas* (*Oxychloe andina*, *Carex incurva*, *Scirpus atacamensis*), often with grasses (*Deyeuxia* spp., *Festuca scirpifolia*); the dwarf rush *Distichia muscoides*, and showy wildflowers including *Gentiana prostrata*, *Gentianella punensis*, *Calandrinia acaulis*, *Werneria pygmaea*, and many *Astragalus* spp. This is a flora closely allied to that of the highlands of southern and central Peru (Weberbauer 1945).

Cuyo District. This is the vegetation of the high Andes of San Juan, Mendoza and the N of Neuquén, from 4500 to 2200 m descending southward. The winters are very snowy; total preciptation is highly variable but always includes summer thunderstorms. The District is entirely outside the tropics and beyond the influence of the "Bolivian Winter," being dominated instead by the interplay of tropical and subantarctic air masses with traveling storms and fronts. Coirón (*Stipa* spp.) is a climax aspect dominant in much of the District, often associated with perennial *Festuca* and *Poa*. The dominant species of *Stipa* varies geographically. On steep slopes shrubs are common, including *Adesmia pinifolia*, *Ephedra andina*, *Berberis empetrifolia*, *Senecio uspallatensis*, *Mulinum ovalleanum*, etc. Typical herbaceous species include *Menonvillea cuneata*, *Nassauvia lagascae*, *Tropaeolum polyphyllum*, and, in *vegas*, the dwarf rush *Andesia bisexualis*, *Plantago barbata*, and *Senecio breviscapus*. Streams are often bordered by *Cardamine nivalis* and there may be a turf of *Hordeum secalinum* or *Agrostis glabra* with *Hypsela oligophylla* and *Werneria pygmaea*. The classic description is by Hauman (1919). A useful modern treatment of the flora is Wingenroth and Suárez (1983).

There is a remarkably rapid floristic and vegetational gradient from N to S in the *Cuyo*. The northern part of the *Cuyo* forms a transition from the tropical climates to the N, dominated by rainfall seasonality but with no true winter, to the strongly temperate-seasonal climates in Mendoza with a pronounced winter snow pack. By the latitude of Las Leñas and Cerro Sosneado the climates and aspect have become decidedly more Patagonian. These gradients are reflected from the high desert to the high alpine in the presence of species-level endemics among flowering plants and butterflies. Because of its easy accessibility, the vicinity of the Paso Bermejo is often taken as "typical" of the montane *Cuyo*, thereby underestimating the high diversity within the District.

Austral District. From C and SW Neuquén southward at ever-decreasing elevation, the high-Andean flora descends and mixes with Gondwanaland (subantarctic) elements, especially in the more humid areas. Steppes are often dominated by *Poa obvallata* and *Festuca weberbaueri* or *F. monticola*, the marshy meadows by *Deyeuxia*, *Deschampsia*, and *Poa*, and especially in the far S, crowberry (*Empetrum rubrum*) becomes conspicuous or dominant on poor (sandy, sterile, and boggy) sites. The communities of Tierra del Fuego, which partake of this District but also of the Subantarctic Domain, are well-described in Moore (1983).

Puna Province. The Argentine *puna* occurs from 3400 to 4500 m, from the Bolivian border to NE Mendoza, where it can be found in dilute form to 2000 m. The climate is dry and cold, with mean annual temperature of 7.5–9.9°C and annual precipitation from 324 mm at La

Quiaca to 103 mm at San Antonio de los Cobres, to nearly zero at the Chilean border.

The *puna* is a xerophytic high-altitude shrub-steppe dominated by *tola* (*Parastrephia lepidophylla*) and river *tola* (*P. phylicaeformis*) where ground-water levels are fairly high. Many other species occur (*totilla, Fabiana densa*; *chijua, Psila boliviensis*; *anagua, Adesmia horridiuscula*; etc.) along with dwarf cacti (*Opuntia soerensii, Oreocereus trollii*, etc.). Some other characteristic species are *Pennisetum chilense, Scirpus atacamensis, Juncus depauperatus, Plantago tubulosa, Hypsela oligophylla, Festuca scirpifolia, Bouteloua simplex, Muhlenbergia fastigiata, Trifolium amabile, Astragalus bustillosi, Ipomoea minuta*, etc. Farther W, in Chile, extensive flat bogs occur within the *puna*. The classic description is Cabrera's (1958) monograph.

Comment on the High-Altitude Vegetation in Salta, Jujuy and Tucumán. — The Argentine NW is vegetationally very complex, as Figs. 6 and 7 demonstrate. The upper reaches of the Yungas grade into *prepuna, puna*, and Quichua high-Andean vegetation and the formation is exquisitely dependent on slope, exposure and in some cases, substrate. As noted below, many of the high-altitude butterfly species appear to have very specific requirements within this complex mosaic, but may be widespread where their particular microclimates occur. This is characteristic of tropical organisms, while temperate species tend to be more broadly distributed both ecologically and geographically (Stevens 1989). A notable exception is *Tatochila mercedis macrodice*, which seems to transcend formation or association boundaries, occurring nearly everywhere at high altitude.

Patagonian Province. The first hints of Patagonian vegetation appear in the *precordillera* of Mendoza. The transition from the *Monte* and *Cuyo* to Patagonia occurs gradually from Chos Malal, Neuquén S through Loncopué to Zapala. In the N of this transition zone the *mallines* are nearly or quite pure Patagonian while the nearby hills have an increasing proportion of Patagonian species with both latitude and altitude.

The traditional "political" boundary of Patagonia is the Río Negro, but Patagonian floristic elements occur N in the W of the region, while elements of the *Monte* reach even beyond Comodoro Rivadavia on the Atlantic shore. The precise location of the boundary of the Patagonian Province is controversial (cf. Soriano 1949, 1956, Ragonese and Piccinini 1969). Soils are sandy or gravelly — much of the Province is covered with a thin pavement of gravel washed out from the glaciers — and the climates are cold and dry with winter snow, frosts much of the year, and very persistent strong winds which are perhaps the most characteristic feature. The temperature varies from an annual mean of 13.4° at Chos Malal to about 5° at Río Grande, NE Tierra del Fuego;

precipitation ranges from 100–270 mm over the Patagonian steppe, but rises very rapidly to the W as the continental divide (=border with Chile) is approached. The dominant plant communities are shrub-steppe and bunchgrass steppe. Cabrera recognizes six Districts (but see Boelcke 1957):

Payunia District. This is the *Monte*-Patagonia ecotone in the far N, characterized by *solupe* (*Ephedra ochreata*), the composite *Chuquiraga rosulata*, *Lycium chilense*, *Grindelia chiloensis*, *Junellia seriphioides* and, locally in cool sites, *neneo* (*Mulinum spinosum*), the most distinctively Patagonian element. The unusual Umbellifer *Hydrocotyle*, of subtropical origin, occurs along slow streams — its only occurrence in the Province.

Western District. This is a narrow fringe of shrub-steppe, from northern Neuquén to NE Santa Cruz, dominated by *Mulinum spinosum*, *Trevoa patagonica*, *Colliguaya integerrima* and *Nassauvia axillaris*, with local *coironales* (bunch-grass prairies) of *Stipa humilis*, *neaei* and *speciosa* often containing *Poa huecu*, *Bromus macranthus*, *Festuca argentina*, etc., and more or less saline seeps or marshes with *Distichlis scoparia* and *D. spicata* and bulrush marshes (*Scirpus californicus*). Pampas-grass (*Cortaderia* spp.) reaches its southern limits here, often in overgrazed bottomlands just upslope a few cm from *mallines* of *Distichlis*.

Central District. This is the most arid part of Patagonia, from the center of Río Negro through most of Santa Cruz. The predominant steppe species are *quilenbai* (*Chuquiraga avellanedae*), *colapiche* (*Nassauvia glomerulosa*), and *coirón amargo* (*Stipa humilis*, *neaei* or *speciosa*); associates include *Ameghinoa patagonica*, *Nardophyllum obtusifolium*, and *Brachyclados caespitosus*. In the far S, *quilenbai* drops out and is replaced by *mata negra*, *Junellia tridens* (Verbenaceae, not to be confused with other shrubs having the same common name in other regions). Saline marshes are dominated by *Atriplex lampa*. In moist gullies larger shrubs such as *Anarthrophyllum rigidum*, *calafate* (*Berberis cuneata*), *Senecio filaginoides* and *Lycium chilense* occur.

San Jorge District. This is a "warm pocket" along the Gulf of San Jorge in the vicinity of Comodoro Rivadavia, where *Monte* elements including creosote bush can be found. Characteristic dominants are *Trevoa patagonica*, *Colliguaya integerrima*, *Stipa humilis*, *Mulinum spinosum*, *Adesmia campestris*, *Anarthrophyllum rigidum*, *Festuca pallescens* and *argentina*, etc.

Subandean District. This is the lower fringe of the Patagonian Andes proper, widening out S of 51° to reach the Atlantic. Annual precipitation is 200–350 mm; the climate is humid at least part of the year, even the dry season is rather cloudy due to high-altitude moisture transported over the Andes by the prevailing westerlies and formed

into extensive wave altocumulus in their lee, and the soils are richer and more mature than in areas further NE. The climax vegetation is *Festuca pallescens* steppe, with a very long list of associates including *Poa ligularis*, *Bromus macranthus*, *Elymus patagonicus*, *Calceolaria polyrhiza*, *Acaena pinnatifida*, *Viola maculata*, *Lepidophyllum cupressiforme*, etc.

Fuegian District. This is the NE of Tierra del Fuego, extending to the transition from steppe to *Nothofagus* forest SW of Río Grande. *Festuca gracillima* is the dominant steppe grass. Many characteristic and showy wildflowers occur, of which *Primula magellanica* and *Oxalis enneaphylla* and *fueguensis* are characteristic.

Subantarctic Domain and Province. Characterized by the dominance of south-end-of-the-world (Gondwanaland) taxa of great antiquity, adapted to cool and moist, temperate climates — *Nothofagus*, *Dacrydium*, *Fitzroya*, Myzodendraceae, Desfontainaceae, Tetrachondraceae, Donatiaceae, etc. This Domain is mainly W of the Andean crest in Chile. Four distinct Districts are recognized by Cabrera; their relationships are clearer when the vegetation map of Chile is consulted along with that of Argentina.

Pehuénia. The relict forests of Pehuén, *Araucaria araucana*, from Volcán Copahue to Lake Lolog in western Neuquén, from 900–1800 m, associated with *Nothofagus pumilio*, *Chusquea culeou*, *Berberis buxifolia*, *Pernettya mucronata*, *Maytenus disticha*, *Ribes magellanica*, *Escallonia virgata*, *Nardophyllum obtusifolium*, *Cortaderia pilosa*, *Chlorea alpina*, *Acaena pinnatifida*, etc. — marking the N limits of many species, and diluting gradually to the E in the San Martín–Junín–Aluminé region until only occasional *Araucaria* are superimposed on bunchgrass steppe; such sites are often called "Primeros Pinos."[3]

Deciduous Forest District. The forests of *Nothofagus pumilio* and *antarctica* and of *Austrocedrus chilensis* extend to tree-line above and steppe below, with a complex structure of communities or associations. In the far N *Nothofagus procera* and *obliqua* also occur. The *coligüe* bamboo, *Chusquea culeou*, is locally very abundant, as on Cerro Catedral near Bariloche. Wildflowers are numerous and include *amancay*

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[3] The easternmost stand of *pehuenes* is located on the Espinazo del Zorro along Highway 46, SW of the Laguna Blanca National Park in Neuquén. It very clearly indicates a much more mesic climate eastward within the past 1000 yr or so. The genus *Araucaria* was formerly much more widespread, both globally and in South America, and has been in decline since the early Tertiary. The Olsacher Museum of Geology in Zapala, Neuquén has an excellent collection of fossil *Araucaria* material from the region. The complete lack of a distinctive butterfly fauna associated with the *pehuén* vegetation is striking.

(*Alstroemeria aurantiaca*), *Codonorchis lessonii*, *Mutisia spinosa* and *decurrens*, etc. Like the preceding, this District is defined by relicts whose distributions reflect very local, topographically-mediated microclimates E of the crest.

Valdivian District. This is the true cool-temperate Tertiary rainforest of S Chile, floristically extremely rich but dilute on the Argentine side of the border where it penetrates only in the far W of the Lanín, Nahuel Huapí, and Los Alerces National Parks. Precipitation in some places reaches 4000 mm/yr. It has two characteristic butterflies: the Pierid *Eroessa chiliensis* and the Hesperiid *Argopteron aureipennis* Butl. See Ringuelet (1955).

Magellanic District. The southern beech forests (*Nothofagus*) and associated *Sphagnum*-bog (*turbal*) habitats of Tierra del Fuego (Moore 1983).

Comment on the Vegetation of Patagonia and Fuegia. These parts of Argentina have engendered an immense literature. Besides Cabrera, an excellent overview in English, with comparisons to North America, is to be found in Beetle (1943). Dimitri (1962) reviews the flora, and (1972) sets it in a regional and physiological context.

Cabrera's classification and mapping are necessarily somewhat typological. Even so, it is evident that the Districts are not very well-defined and the lines demarcating them are at best approximations of statistical changes in community composition. The intimate interdigitation of subantarctic and Patagonian elements makes line-drawing in the far S quite arbitrary. My experience suggests that the distribution of Satyridae in Patagonia may be studied profitably with respect to plant community patterns. The Patagonian and Fuegian Satyrids have been monographed by Heimlich (1972).

Among numerous accounts of Patagonia, Lista (1896a, b) and Willis (1914) are particularly instructive in enabling us to assess the amount of vegetational change due to the activities of the white man. It is quite evident, especially from Willis, that the extent of *Nothofagus* forest has been greatly reduced by cutting, burning and conversion to pasturage. Given that many evolutionarily interesting and important phenomena are today occurring in zones where such conversion occurred in the last century, it is important to keep this in mind. The W of Neuquén and Río Negro and the vicinity of the Gulf of San Jorge rank with the W of Salta and the *Sierras Pampeanas* as regions of special concern for butterflies; the mainland-Fuegian transition, in particular the littoral from Comodoro to Río Grande, will also require further attention. Very rapid urban growth in the far S since 1970 is already impacting butterfly habitats.

Systematic Treatment

Collection abbreviations are identified in the Acknowledgments section.

Genus *Theochila* Field

Theochila maenacte Boisuval

Theochila is probably the sister-genus of the non-Crucifer-feeding part of the large genus *Tatochila*, which will almost certainly be divided in two or three genera once sufficient species have been reared. *Theochila* is defined by a variety of odd autapomorphies (Field 1958). The single species *maenacte* is divided into two allopatric subspecies. Its distribution (Brown 1987, Fig. 4.18) is part of a repeating pattern of faunal and floral connections between the Andes and Serra do Mar/SE Brazil, which "leaves no doubt that links of suitable vegetation and humid temperate climate existed across northern Argentina in the distant past" (Brown 1987, p. 95; O. Mielke, pers. comm.).

The nominate subspecies *T. m. maenacte* differs from the Brazilian *T. m. itatiayae* Foetterle primarily in slightly smaller size and a drastic reduction in the dark wing-pattern in the male, producing an effect not unlike *Pieris rapae* L. Herrera and Field (1959) had little material available and apparently did not recognize that *T. m. maenacte* is seasonally diphenic, with a winter form nearly indistinguishable from *itatiayae* and a very pale summer form on which their redescription was based. The BM contains a very extreme winter male, unfortunately without date, labeled "Buenos Ayres, Elwes 1920." It also has a long series of more or less typical summer specimens labeled "Buenos Aires (Belgrano), 15.XII.1889." The very pronounced seasonal polyphenism of the male and lack thereof in the female (in which the denser thoracic and abdominal pelage, and richer black color in the wing pattern are the only manifestations) parallels the situation in *Tatochila vanvolxemii* = *T. mercedis vanvolxemii* Capronnier. It would be of great interest to determine whether photoperiod or temperature or both influence the polyphenism.

Theochila m. maenacte was formerly common in riparian and marsh habitats in and around Buenos Aires (Riachuelo; Avenida de los Italianos — Zona Portuaria, etc.) but has disappeared or diminished in many sites in the past decade. Until slum clearance and construction of the central bus station destroyed its habitat, it was common behind the Retiro railroad station several blocks from the center of the city, as late as the mid-1970s. It was not found in the "Vida Silvestre" preserve in the Zona Portuaria in XI.–XII.1989. It is still common in marshy sites in Quilmes and south to the vicinity of La Plata, which seems to be its southern limit. The Museo de La Plata contains much local material, e.g. series from La Plata, 27.III.1927; 3♀, 2.XII.1928; an extreme

winter form ♀, 28.X.1928, and a dozen from the northern suburb of Punta Lara, II. 1928, *leg.* R. Maldonado. It is also still locally common in Tigre and the Paraná Delta north of the capital, and should be looked for in the marshes near Ezeiza (the old "Belgrano" locality?)

Genus *Tatochila* Butler

As noted under *Theochila*, this genus appears to be polyphyletic and will probably need to be divided. At present it is the largest Pierine genus on the continent. Since the lines of the division are not yet clear, I am opting for taxonomic conservatism by retaining all of Herrera and Field's (1959) species-group designations within *Tatochila*, whose type-species is *autodice* Hübner.

Tatochila theodice theodice Boisduval (Fig. 8A, D).

The N and S limits of the nominate subspecies have been poorly defined in Argentina. Herrera and Field (1959, p. 478) had little Argentine material available.

3♂ Loncopué, Neuquén, 8.XI.1988 (AMS)

1♂ Catan Lil, Neuquén, 840 m, 16.I.1977 (MG)

The Loncopué record (38°04′S, 70°37′W) probably defines the N limit of both the subspecies and species as it is unrecorded at Chos Malal, which I have collected very thoroughly. The Catan Lil record may represent the farthest E and downslope penetration of the high desert in river bottoms, to which this mesic species is largely restricted in the N of its range. It is clearly resident at Loncopué, and the specimens are of the early spring (post-diapause) phenotype.

The S limit is defined by the transition to ssp. *gymnodice* Staudinger, which is accomplished in gradual, clinal fashion, as demonstrated by the following material:

2♂ 3♀ Lago Argentino, Península Magallanes, Santa Cruz, loc. #28, 11.I.1979 (DE)

6♂ Tecka, Corcovado, Chubut, 750 m, loc. #47, 17.II.1979 (DE)

1♂ La Esperanza, 130 km NW Río Gallegos, Santa Cruz, loc. #30, 15.I.1979 (DE)

Herrera and Field had no material between the Nahuel Huapí National Park, Río Negro (nominate *theodice*) and Río Túnel, Santa Cruz (*gymnodice*), creating a false impression of disjunction. In the Lago Argentino series the females are somewhat more *gymnodice*-like than the males. See Fig. 8B, E.

Tatochila theodice staudingeri Field

Herrera and Field (1959) divide the Fuegian *theodice* into two subspecies, recognizing *gymnodice* from Porvenir, Magellanes (Chile) and *staudingeri* from Puerto Harberton (the type locality) and Ushuaia, both in Argentine Tierra del Fuego, as well as from Isla Navarino,

Magallanes. Again, when sufficient material is assembled, the distinctness of these subspecies disappears.

2♂ 2♀ Cabo Peñas, Depto. Río Grande, T. del F., 17.XII.1983 (ML)
56♂ 30♀ Río Grande, T. del F., 25.XI.1988 (AMS) (Figs. 8C, F)
2♂ Estancia María Cristina, Route 3, T. del F., 27.XI.1988 (AMS)
1♂ 1♀ Base of Monte Susana, Parque Nacional, T. del F., 18.I.1979 (AMS)

A cline exists from NE to SW across Isla Grande de la Tierra del Fuego, corresponding to both precipitation and vegetation gradients. *Staudingeri* phenotypes are increasingly frequent to the SW, but occur even at Río Grande in the extreme NE where populations are immense and variation very pronounced. Herrera and Field fail to note that Fuegian females are dimorphic in ground color: yellow, or white like the males. This is a genetic trait, as established by rearing.

Nominate *theodice* from Río Negro and *gymnodice/staudingeri* from Río Grande, T. del F., have been reared *ex ovo* and descriptions are in preparation. There are subspecific differences in the early stages.

Tatochila autodice **Hübner (including** ***T. blanchardii*** **Butler)**

Shapiro (1986a) demonstrated that *T. autodice* and *T. blanchardii blanchardii* intergrade in NW Patagonia, from Chos Malal, far N Neuquén, to C Chubut, mainly in the ecotone from the forested Patagonian Andes to bunchgrass — shrub steppe. Detailed records are presented there. The farthest S record for apparently pure *autodice* is Puerto Deseado, Santa Cruz, 1♂, 16.I.1967 (A. Willink) (ML). In 1989 I found *T. autodice* common in eastern Patagonia, viz. 1♀ Trelew, Chubut, 7.XII; 2♂ Las Plumas, Chubut, 7.XII; 3♂ Parada Uzcudún, Chubut, 7.XII; 1♀ El Tordillo, Chubut, 8.XII; 1♀ Pampa del Castillo, Chubut, 11.XII; 1♂ 2♀ Caleta Olivia, Santa Cruz, 9.XII; and 1♀ Fitz Roy, Santa Cruz, 9.XII. Both Caleta Olivia ♀ have an unusual yellow ground color but are otherwise typical. None shows any trace of *blanchardii* influence. Three of these localities represent tiny pockets of weedy Crucifers in extensive shrub-steppe, demonstrating the high dispersal capability of this species.

The farthest SE that *blanchardii* influence has been recognized is El Trébol, Chubut, 1♀, 12.II.1967 (A. Willink) (ML). Some intermediate phenotypes from Río Negro and Chubut are shown in Fig. 9. As noted in Shapiro (1986), the intergrading populations in the Lake District are unusually sparse. This is consistent with the now widely-recognized phenomenon of the "hybrid sink" (Barton and Hewitt 1985), although the intergrading population as Esquel is much larger; it is also in a drier climate and has a stronger *autodice* component. It should be noted that the usual host plants of the Lake District populations are native *Tropaeolum polyphyllum* rather than introduced weedy Crucifers, based on censuses done in 1988. At least some of the area occupied by these populations is mapped as recently (turn-of-the-

century) deforested in Willis (1914).

The La Plata collection contains numerous apparently typical *blanchardii* from northwestern Patagonia, viz.: 1♂ Lago Lácar, Pucará, Neuquén, I.1958; 1♀ Lago Hermoso, Neuquén, I.1958; 1♀ Ruca Malen, Neuquén, undated; 1♀ Isla Victoria, Lago Nahuel Huapí, Río Negro, I.1960; 1♀ Quila Quina, Lago Lácar, Neuquén, I.1958; 2♀ San Martín de los Andes, Neuquén, I.1958; and 1♀ Lago Curahue, 950 m, Neuquén, I.1958. There is also one obvious ♂ intergrade, labeled "Río Negro," I.1936 (#2646).

On the basis of this rather extensive if mosaic intergradation I propose treating Herrera and Field's (1959) "*autodice* species group (Group B)" as a polytypic species, viz.:

Tatochila autodice Hübner 1818
Tatochila autodice blanchardii Butler 1881, new combination
Tatochila autodice ernestae Herrera 1954, new combination

Because nominate *autodice* and *ernestae* may be parapatric and altitudinally stratified in the Bolivian *yungas*, *autodice* may be a "ring species" (circular overlap, Mayr 1963, p. 507 *ff.*).

Tatochila mercedis Eschscholtz (including *T. sterodice* Staudinger, *T. fueguensis* Field, *T. macrodice* Staudinger, *T. arctodice* Staudinger, and *T. vanvolxemii* Capronnier)

This is the "*microdice* species group (Group C)" of Herrera and Field (1959). The incorrect use of the name *microdice* was corrected by Ackery (1975). Thereafter the name *sterodice* was used for a polytypic species embracing the taxa *fueguensis*, *macrodice* and *arctodice* — *mercedis* and *vanvolxemii* being treated as separate species. However, all the taxa of this group, from Colombia to northern Fuegia at least, are interfertile in the laboratory and intergrade through fairly sharply-defined hybrid zones wherever they come into contact afield (Shapiro 1979, 1984, 1986b and unpublished). The oldest name in the group is *mercedis* and all the other taxa may be considered subspecies of it. This action was initiated by Lamas and Pérez (1983) in listing *macrodice* as a subspecies of *mercedis*. "Group C," the "*sterodice* species-group" of my earlier papers, thus becomes:

Tatochila mercedis Eschscholtz 1821
Tatochila mercedis macrodice Staudinger 1898
Tatochila mercedis arctodice Staudinger 1898, new combination
Tatochila mercedis vanvolxemii Capronnier 1874, new combination
Tatochila mercedis sterodice Staudinger 1898, new combination
Tatochila mercedis fueguensis Field 1959, new combination

Because of intrinsic problems with the subspecies as a taxonomic category, and because one does not expect to find clear-cut taxonomic situations in groups as evolutionarily active as this one, a certain degree of arbitrariness seems inevitable in ranking the taxa. Cracraft

(1989), writing from one cladistic standpoint, denounces the ontological vacuity of polytypic species, a legacy of the Biological Species Concept, which he rejects. Nonetheless, the reproductive, genetic and geographic data available all appear to argue for polytypic-species status for this group, despite the morphological distinctness of some of its members; I accept the primacy of data over ideology.

The following, hitherto-unpublished data amplify the known Argentine distributions of these taxa and fill in gaps on previously-published maps (Figs. 10A, 11A).

Tatochila mercedis macrodice

Reported occurrences of this taxon in Argentina fall into three geographic regions; the *puna*, the Quichua District, and the Cuyo District.

(i) The *puna* of Jujuy and Salta

R. Eisele states (*in litt.*, 26.I.1978): "...according to Hayward...has been found as far S as Mendoza. In the last few years I have got a number of good series of this in Jujuy and Salta. All come from altitudes from 2450 to 4000 m and most common above 3000 m, at which altitude it is the most common *Tatochila*."

Some specific records:

2♂ Abra de Pives, Jujuy, 3900 m, 3.II.1969 (ML)
18♂ 13♀ Abra Pampa, Jujuy, 7.II.1984 (AMS)
14♂ 8♀ Esquinas Blancas, Jujuy, 7.II.1984 (AMS)
2♂ 31 km N Humahuaca, top Azul Pampa, Jujuy, 12.I.1978 (RE)
3♂ Abra Azul Pampa, Jujuy, 7.II.1984 (AMS)
6♂ Altos de Abra Muñano, Salta, 4165–4780 m, 21.I.1983 (AMS)

(ii) The Quichua District

This entity occurs in the *puna-jalca* alpine vegetation above the *yungas*. It is recorded in two geographic subdivisions:

(a) Salta highlands

3♂ Abra Molina, Salta, 22.I.1986 (AMS), 1♂ 2♀ 28.XI.1989 (AMS)
5♂ Cerro Zapallar, Salta, 22.I.1986 (AMS)
1♂ Valle Encantado, Salta, 3550 m, 14.XII.1976 (ML)

(b) The *Sierras Pampeanas* (Cumbres Calchaquíes, Sierra de Aconquija)

1♀ Cerro de la Mina, Depto. Tafí, Tucumán, IV.1933 (K. Hayward) (ML)
1♂ "Aconquija", 11.III.1917 (P. Jörgensen) (BM)
1♀ Esquina Grande, Catamarca, 1640 m, 30.XI.1915 (BM)
2♀ "Tucumán, 2000 m," III.1905 (J. Steinbach) (BM)
2♂ 1♀ Tafí del Valle, Tucumán, 2150 m, 30.XI.1977 (AMS)
3♂ Abra Infiernillo, Tucumán, 20.I.1986 (AMS), 2♂ 26.XI.1989 (AMS)

Specimens from the *Sierras Pampeanas* appear to average slightly smaller and more heavily marked than the others. Except for a

genetically-determined ground-color polymorphism (white *vs.* yellow, white dominant — AMS, unpublished data) found in most populations, *macrodice* is extremely constant over its entire range in Peru, Bolivia, Chile and Argentina.

Like many butterflies of the *puna* and upper *yungas*, *T. m. macrodice* appears to migrate altitudinally with the season. It is present at lower altitudes in dry season than at other times, and disappears entirely from the vicinity of Tafí del Valle in January. However, as the 1989 data show, it emerges immediately in the highlands of both Salta and Tucumán with the onset of the rainy season in November, flying even before the vegetation has greened up. It thus must be 2- or more likely 3-brooded in the highlands, passing the dry season as a pupa, but no trace of diapause exists under laboratory conditions.

(iii) The Cuyo District

I have not found the documentation for the Hayward citation mentioned by Eisele. He did not include Mendoza for this entity in his (1950) *Catalogo Sinonímico*...but did in the posthumously-published 1973 catalog (p. 114). This reference also lists San Luis, a lowland Province whose highest point (in a pre-Andean range) is under 2000 m and which is unlikely to have any *macrodice* habitat at all. This suggests some kind of confusion existing in Hayward's mind late in his life concerning the identity of *macrodice*, and it is not hard to find evidence for this in museums. Herrera and Field (1959) record a specimen of *macrodice* from "Funes, Mendoza, January" which is the only precise locality ever published from Mendoza, but I have been unable to trace either the specimen or the locality. There is no "Funes" (or "Deán Funes") in Mendoza in available maps (Automóvil Club Argentino, sections 3 and 5, Carta Turística, 1969–72) or gazzetteers (US Department of Interior 1968).

ML contains a small female *vanvolxemii* from Potrerillos, Mza., 1500 m, 1947 (Hayward and Willink), misidentified as *macrodice*. La Plata has much more. Under *macrodice* (box 297) are 7♂ 4♀ from Potrerillos, X.1951. In addition, likewise identified as *macrodice* by Hayward, one finds a ♂ from Los Corrales, La Rioja, 1935 (lot #2643) (box 312) and a female without locality, "Junio 1925". All of these are *vanvolxemii*. Most are heavily marked, winter-spring forms. The *vanvolxemii* at Potrerillos may have some *mercedis* introgression and are undersized in summer. Also in La Plata are 1♂ 1♀ from Potrerillos (also X.1951) which were determined by Field as *vanvolxemii* but bear a handwritten label: "Opina Field que son intermedio de *microdice macrodice* o híbridos de éstos" ("Field opines that these are intermediate to *macrodice* or hybrids with it"). (See Porter and Shapiro 1990 for discussion of the Potrerillos population.) There is no current basis for recording *macrodice* in the Cuyo.

I have a single, highly unusual male from the highlands of San Juan which is in some ways intermediate between *macrodice* and *sterodice*

or *mercedis*. Its data are: Arroyo de Agua Negra, 3300 m, 3.XI.1988 (AMS). The pattern is more or less midway between *macrodice* and *mercedis* (Fig. 12); the scales behind the eyes are white (as in *mercedis* or *sterodice*) rather than orange (as in *macrodice*); its compound eyes in life were gray-green, intermediate between the gray-blue of *sterodice* or *mercedis* and the bright chartreuse-green of *macrodice*, and unlike any other *Tatochila* I have examined alive in nature; and its genitalia, examined only externally, appeared to be arranged as in *sterodice* or *macrodice* rather than as in *mercedis*. I interpret this individual as possible evidence for a transition from *macrodice* to *mercedis* in the very-poorly-collected zone of transition from the Quichua to the Cuyo District.

Given the amount of collecting done in the vicinity of the Paso Bermejo (Las Cuevas, Punta de Vacas, Puente del Inca) in the past century, if *macrodice* occurs in that easily accessible locality in the *cordillera* of Mendoza it must be either at very low density or at altitudes above 4200 m, which are less well-known. I did not find it there (up to 4350 m) in six days in XI–XII. 1989.

Tatochila mercedis vanvolxemii

The winter form of this widespread and common entity shows the complete *sterodice* pattern in the male. As only reared (experimental) examples have been figured heretofore, and then not in systematic or biogeographic works, I provide (Fig. 13) wild-collected ones from the "core" range where introgression from other subspecies is highly unlikely.

The NW limits of *vanvolxemii* have been in question. It has often been cited from "Tucumán," which is usually (and often wrongly) interpreted as referring to the capital, San Miguel de Tucumán, where it definitely does *not* occur (and has not in historic times). The only definite records I have from the Province of Tucumán are from Amaichá del Valle: 4♂ 3♀, 4.II.1984 and 1♀, 26.XI.1989 (all AMS). Amaichá, on the dry side below Abra Infiernillo en route to the Valles Calchaquíes, is a high-desert locality. More or less similar habitat occurs up the Valles Calchaquíes (Río Santa María drainage, the N-most extent of the *monte*) as far as the vicinity of Cachi, Salta where I have collected only *T. autodice* and *Ascia monuste automate* Burmeister. Thus we may infer that *vanvolxemii* follows the *monte* to near its N limit but does not extend into the *prepuna*. If *T. m. vanvolxemii* is a permanent resident at Amaichá it is spatially very close to *T. m. macrodice*, though altitudinally and ecologically segregated. Our samples from Amaichá are very small to detect introgression from *macrodice*. Two of the females are unusually heavily-marked, and one is the darkest *vanvolxemii* I have seen. The XI.1989 female is old and worn but vaguely suggestive of *macrodice* influence. It does seem cer-

tain that there is no extensive intergradation, such as occurs farther south in this polytypic species.

Populations of apparently pure *vanvolxemii* occur at low-elevation, desertic sites quite close to the zone of intergradation with *sterodice* and *mercedis* in NW Patagonia. Examples are:

2♂ Covunco, 820 m, Neuquén, 12.XI.1966 (MG)

2♂ 1♀ Estancia Corral de Piedra, Collón Curá, Neuquén, 650 m, 3.XII.1969 (MG)

1♂ Las Lajas, Neuquén, 730 m, 15.I.1980 (MG)

The Collón Curá series includes both extreme winter forms and intermediates to the summer form. A similarly mixed series was taken at Zapala, Neuquén, 9–11.XI.1988 (AMS). This is also a pure population. The occurrence of winter forms as late as early December at low altitude is fairly unusual; they normally occur only in the first brood. Control of the polyphenism is discussed in Shapiro (1980a).

Typical *vanvolxemii* (averaging small) are abundant in eastern Patagonia as far south as Trelew (18♂ 5♀, 7.XII.1989), Las Plumas (43°43'S, 67°15'W, 11♂ 6♀, 7.XII.1989), and Parada Uzcudún (44°13'S, 66°09'W, 17♂ 17♀, 7.XII.1989) (all Chubut, all AMS). At Trelew oviposition was observed on *Cardaria draba* (L.) Desv. (Cruciferae), usually a disfavored Pierid host.

Records of *T. m. vanvolxemii* from "Buenos Aires" have always been ambiguous due to confusion of the city and the Province. On 23.XI.1989 it was common in the city (Costanera Sur, Avenida de los Italianos, Zona Portuaria, vacant lots in La Boca), the first time I have seen it there.

Hybrid Zones involving *T. m. vanvolxemii*

2♂ 13♀Loncopué, Neuquén, 8.XI.1988 (AMS)

This remarkable series marks a new N limit (38°04'S) for the zone of intergradation, or hybrid zone, between *vanvolxemii* and other entities. Although very close to Aluminé (39°13', 70°57'W), this population is phenotypically very different. The Aluminé population shows no significant *vanvolxemii* component, while that at Loncopué is mostly *vanvolxemii* (by phenotype). The females are most like *vanvolxemii*, with variable *sterodice* influence. The two males differ astonishingly from each other: one resembles the putative *sterodice-vanvolxemii* hybrid from Bariloche figured by Shapiro, 1980a (which in turn resembles series of this cross, reared in the laboratory under summer photoperiod/temperature regimes); the other resembles a winter form of *vanvolxemii* below and a *sterodice-mercedis* intergrade with strong sagittate pattern above. All of these (Fig. 14) were taken flying together in one pasture. The host plant is *Lepidium* sp. (Cruciferae).

Loncopué is, as noted above, the N-most locality known for *T. theodice*

in Argentina. It is also the N-most locality for the skipper *Hylephila signata* Butler and the third most N for *Colias vauthierii* Guérin, discussed later. Both of these are typical Patagonian *mallin* species which rarefy progressively as one moves N into the transition to the *cuyo*.

22♂ 11♀ Barrio Próspero Palazzo, Comodoro Rivadavia, Chubut, 19.XI.1988 (AMS) Several previous collections from Comodoro Rivadavia (San Jorge District) (45°52′S, 67°30′W) were made in high summer and had produced the erroneous impression that the population there was pure *vanvolxemii*. As noted above, summer *vanvolxemii* lose most or all of the black pattern in the male, and this is the summer phenotype at Comodoro. This large series of the first (ex diapause), spring generation — in which the pattern is fully expressed — reveals a strong apparent admixture of *sterodice* genes (most apparent in the dotted DFW pattern, which is almost never seen in *vanvolxemii* in its "core" range far from hybrid zones). A few of these Comodoro males would unhesitatingly receive *sterodice* labels if considered out of context.

In 1989 a systematic attempt was made to map the distribution of intergrading populations in eastern Patagonia. Populations very similar to that at Comodoro were found at: El Tordillo (45°53′S, 67°57′W, 6♂ 5♀, 8.XII); Pampa del Castillo (45°48′S, 68°65′W, 13♂ 7♀, 11.XII), both Chubut; Caleta Olivia (46°26′S, 67°32′W, 9♂ 6♀, 9.XII) and Fitz Roy (47°02′S, 67°15′W, 25♂ 7♀, 9.XII), both Santa Cruz (all AMS).

The seasonal polyphenism of *vanvolxemii* is expressed in the San Jorge region superimposed on a mixed genetic background. This phenomenon, as noted above, is best detected in the spring brood and it remains to be seen if these populations differ among themselves in the strength of the polyphenism. The occurrence of the intermediates here is consistent with the anomalous climatic and vegetational character of the San Jorge District, reflected also in the abundance of *T. a. autodice*, *Colias lesbia*, and other species much farther south than they occur in the interior. Between Fitz Roy and Comandante Luís Piedrabuena all trace of *vanvolxemii* phenotype disappears. Although I have visited both San Julián (49°18′S, 67°43′W) and Puerto Deseado (47°45′S, 65°54′W), I have collected no *Tatochila* due to bad weather. ML, however, contains a Puerto Deseado male which if anything shows a transition from *sterodice* to *fueguensis* phenotype, certainly nothing of *vanvolxemii*. MLP contains 3 San Julián specimens which appear to be pure *sterodice*. All trace of *vanvolxemii* also disappears between Pampa del Castillo and Sarmiento (45°36′S, 69°05′W).

Fig. 15 demonstrates the variation in the first brood at Comodoro.

MLP also contains a ♀ from San Martín de los Andes, Neuquén, 2.I.1958, which resembles closely a lab F_1 hybrid between *mercedis* and *vanvolxemii* (not involving *sterodice*).

Tatochila mercedis sterodice

Populations of *T. m. sterodice* are extremely variable even when not plainly involved in intergradation with other taxa; indeed, there are few characters which are sufficiently constant throughout its range as to be diagnostic. Thus, singletons or short series are of limited use in characterizing geographic patterns of variation. The range of variation is, however, broader still in zones of contact with other taxa, and numerous novel phenotypes not seen elsewhere occur there. When in contact with nominate *mercedis* in NW Patagonia, *sterodice* displays lability in genitalic morphology as well as in wing pattern. Elsewhere, its genitalia are constant (Porter and Shapiro 1989).

The following short series all appear to fall within the "normal variation" displayed by "pure *sterodice*." The Valle Lago Blanco series is especially variable, and one specimen from there (reported below) appears to be a hybrid with *mercedis*. The neotype of *sterodice* designated by Ackery (1975) is singularly unfortunate in being at the heavily-marked end of the "normal variation" spectrum. Moreover, the entire type-series of *sterodice* came from within the zone of intergradation to *fueguensis*, in the far S of the range of *sterodice*. The synonym *allodice* Bryk, from LLau-LLau (near Bariloche) would make better geographic sense!

1♂ Estancia Huechahue, Neuquén, 14.XI.1988 (AMS)
2♂ Chapelco, 1750 m, Neuquén, 20.II.1973 (MG)
1♀ Arroyo Chapelco Grande, Neuquén, 900 m, 15.XII.1970 (MG)
1♂ Cordón Chapelco, Portezuelo Trahunco, 1750 m, Neuquén, 27.XII.1978 (MG)
3♂ Refugio Graeff, Parque Nacional Lanín, Neuquén, 1750 m, 12.III.1980 (MG)
1♂ Lago La Kika, Neuquén, 1750 m, 24.I.1979 (MG)
1♂ Quila Quina, Lago Lácar, Neuquén, I.1958 (MLP)
4♂ Pulmarí, Río Alumine, Neuquén, 4500′, Feb.1902 (H. J. Elwes) (BM)
1♂ Bariloche, Río Negro, III.1948 (Williamson & Martínez Fontes) (MR)
1♂ Parque Nacional Nahuel Huapí, Dec. 1912 (BM)
1♂ Puerto Blest, Lago Nahuel Huapí, Río Negro, 770 m, loc. #8, 1.III.1979 (DE)
1♂ Cañada León, Chubut, no date (MLP)
1♂ Alto Río Senguerr, Chubut, 18.XI.1988 (AMS)
1♂ Colonia Sarmiento, Chubut, 600 m, loc. #46, 15.II.1979 (DE)
4♂ Tecka, Gobernador Costa, Chubut, 600 m, loc. #23, 7.I.1979 (DE)
1♀ Tecka, Chubut, 3000′, Jan.–Feb. 1920 (BM)
2♂ 1♀ Valle Lago Blanco, Chubut, "Thursby 1904–26" (BM)
1♂ 1♀ Glen Kross, Santa Cruz, II.1938 (MLP)
1♂ Lago Argentino, Península Magallanes, Santa Cruz, loc. #28, 1.II.1979 (DE)

3♂ San Julián, Santa Cruz, no date (MLP)
1♂ Cte. Luís Piedrabuena, Santa Cruz, 20.XI.1988 (AMS)
1♂ Lago Onelli, Santa Cruz, II.1953 (MLP)

Tatochila mercedis fueguensis

Herrera and Field (1959, p. 488) state that this is "probably most distinct" among the subspecies of "*microdice*" (=*sterodice*). Once again this impression was an artifact of lack of far-S material. Such material, once assembled, demonstrates an unequivocal and relatively even cline from *sterodice* to *fueguensis* phenotypes. The following records represent elements of that cline. Although some individuals are "typical" *fueguensis*, none of the longer series is, and some of the La Esperanza material *from the mainland* is phenotypically indistinguishable from topotypical *fueguensis* (Fig. 16).
2♂ 4♀ La Esperanza, Santa Cruz, 130 KM NW Río Gallegos, loc. #30, 15.I.1979 (DE)
1♂ Perito Moreno, Río Fénix, Santa Cruz, XII.1982 (J. Carreras) (MR)
3♂ Estancia La Cristina, near Lago Argentino, Santa Cruz, 8.II.1953 (A. Willink) (ML)
1♂ Puerto Deseado, Santa Cruz, 16.I.1967 (A. Willink) (ML)
1♀ Cantería Masci, Río Gallegos, Santa Cruz, 22.XI.1988 (AMS)
3♂ Río Gallegos, Santa Cruz, 10.II.1979, loc. #31 (DE)
3♂ 6♀ Río Gallegos, Santa Cruz, 23.I.1979 (AMS)
2♂ Lago Fagnano, Tierra del Fuego, 100 m, loc. #33, 19.I.1979 (DE)

Tatochila mercedis mercedis

The location of the zone of intergradation between *sterodice* and *mercedis* has been documented previously (Shapiro, *loc. cit.*) but the following hitherto unpublished records are of interest because they fill in gaps, or because they demonstrate that hybridization has been in progress for at least several decades.
(a) Apparent hybrids or intergrades
1♂ Cerro Malo, 1700 m, Neuquén, 15.II.1954 (S. Schajovskoy) (MR)
1♂ 1♀ San Martín de los Andes, Neuquén, XII.1952 (S. Schajovskoy) (MR)
1♂ Pucará, Neuquén, 13.III.1960 (S. Schajovskoy) (MR)
1♀ Pucará, Neuquén, 19.III.1960 (S. Schajovskoy) (MR)
1♂ Refugio Graeff, Parque Nacional Lanín, Neuquén, 1750 m, 2.I.1980 (MG)
1♂ San Martín de los Andes, Neuquén, 5.XI.1979 (MG)
1♀ San Martín de los Andes, Neuquén, 640 m, 6.I.1978 (MG)
1♀ San Martín de los Andes, Neuquén, extreme winter form, 15.XI.1969 (MG)
1♂ San Martín de los Andes, Neuquén, I.1958 (MLP)
1♀ San Martín de los Andes, Neuquén, 1.II.1939 (MLP)

1♂ 1♀ Lago Lácar, Pucará, Neuquén, 750 m, loc. #9, 1.XII.1978 (DE)
3♂ 1♀ Quila Quina, Lago Lácar, Neuquén, I.1958 (MLP)
1♂ Aluminé, Neuquén, 1200 m, loc. #57, 14.III.1979 (DE)
1♂ 2♀ Estancia Aschieri, below Primeros Pinos, Neuquén, 1130 m, 9.XI.1988 (AMS)
1♂ El Bolsón, Lago Puelo, Río Negro, Loc. #13, 26.II.1979 (DE)
1♂ "Chile (*sic*), El Bolsón," no date (A. Kovacs) (BM)
1♂ Valle Lago Blanco, Chubut, "1904–26", #10316 (BM)
(b) Indistinguishable from Chilean *mercedis*
1♂ Pucará, Neuquén, 22.I.1958 (S. Schajovskoy) (MR)
1♂ 1♀ Pucará, Neuquén, 15.II.1956 (S. Schajovskoy) (MR)
1♂ Caviahue, Neuquén, 1500 m, 25.II.1962 (S. Schajovskoy) (MR)
1♂ Lago Lácar, Pucará, Neuquén, 750 m, loc. #9, 1.XII.1978 (DE)
1♀ Quila Quina, Lago Lácar, Neuquén, I.1958 (MLP)
1♂ 1♀ San Martín de los Andes, Neuquén, II.1939 (MLP)
1♂ San Martín de los Andes, Neuquén, I.1958 (MLP)
1♀ San Martín de los Andes, Neuquén, III.1952 (S. Schajovskoy) (MLP)
(c) Miscellaneous

The following specimen appears to be a complex hybrid involving *vanvolxemii*, *mercedis* and *sterodice*; it matches certain laboratory-reared hybrids of that composition almost exactly:
1♀ Pulmarí, Río Aluminé, Neuquén, 925 m, 27.II.1978 (MG)

Interspecies Hybrids

The following may be a unique hybrid of *T. a. autodice* and *T. m. vanvolxemii*, showing a mix of characters of both. Both putative parents occur at the site. They are in fact sympatric over nearly half the country, so hybrids must be extremely rare since this is the only suspected one yet found. This hybrid has not been produced in the laboratory.
1♂ Las Lajas, Neuquén, 730 m, 15.I.1980 (MG)

"Group D" *Tatochila* (the "*orthodice* group")

This is a heterogeneous and possibly not monophyletic group. Ackery's (1975) work has increased our knowledge of the central-Andean members of this group, but species limits remain very poorly defined and some of his assignments of subspecies to species may be incorrect. The entire group may be Legume rather than Crucifer specialists. In Argentina they extend only barely to Córdoba; most species are found in the *Yungas* and Quichua District.

Tatochila inversa Hayward (Fig. 17A, B, Plate IV)

Herrera and Field (1959) figured as the male of this species something from the Department of Cusco, Peru. Whether this is really

inversa remains uncertain, but true *inversa* males are now available from various localities in northwestern Argentina. They differ phenotypically among populations and perhaps between broods as well (Fig. 17, from the *puna*; Pl. IV, from the *Sierras Pampeanas*) but differ from Herrera and Field's specimen in a number of details. The species is not rare on summits within the *puna*. The type locality — Quebrada Carapunco — is near Abra Infiernillo in the *Sierras Pampeanas* of Tucumán. Animals from these ranges average larger than those from elsewhere. If a subspecies name is ultimately necessary it would apply to the smaller phenotype from Salta and Jujuy.

Eisele writes (*in litt.*, 26.I.1978): "Just got my first female (*inversa*) from the mountains in Salta. I had previously got a number of males from Jujuy." One of these is figured: Huacalera, N end Cerro Amarillo, Jujuy, 3250 m, 4.I.1980 (RE). Other records: Abra Infiernillo area, Tucumán, 1♂, 26.XI.89, 3♀, 20.I.1986 (AMS); 1♀ Cerro Zapallar, 3720 m, Salta, 22.I.1986 (AMS); 1♀ Abra Azul Pampa, Jujuy, 23.I.1986 (AMS).

The Infiernillo records suggest that this species may be multiple-brooded. The 26.XI.89 male was taken at the very beginning of the rains, before the vegetation had resumed growth.

Tatochila orthodice Weymer

This is a well-known and common species of N Argentina and adjacent Bolivia, essentially restricted to the *yungas*. Most records are low-to-mid montane. It is not generally recognized as a component of the high-Andean fauna but in fact occurs there seasonally in January, flying with *T. m. macrodice*, *T. inversa*, *T. distincta*, etc. This altitudinal migration occurs at the *yungas-puna* and *yungas*-Quichua District interfaces, including the *Sierras Pampeanas*. Some high-altitude records: 1♀ Abra Infiernillo, summit near 3800 m, 20.I.1986 (AMS); 2♂ 1♀ Valle Encantado, 9725′, Salta, 22.I.1986 (AMS); 2♀ Cerro Zapallar, 3700 m, Salta, 22.I.1986 (AMS). At the time these were collected, no *orthodice* were flying in the foothills just above San Miguel de Tucumán, where the species is typically abundant in spring (Anta Muerta, 26.XI.1977; El Siambón and Sala de San Javier, 26.XI.1977, all AMS). I have a mid-elevation record seasonally inbetween these (Tafí del Valle, 2200 m, 26.XII.1977, AMS).

This species was common at La Viña, Catamarca, 29.XI.1989 (AMS).

Tatochila stigmadice Staudinger

Also best-known as a foothill *yungas* species, *T. stigmadice* occurs occasionally in the high country in summer and also as low as the city of San Miguel de Tucumán. My extreme records are: 1♀ Cerro Zapallar, 3600 m, Salta, 22.I.1986 (AMS); 2♂ Barrio Fray Usquiu, S.M. de Tucumán, 450 m, 28.XI.1977 (AMS); I♂ San Miguel de Tucumán

(centro, along R.R. track), 29.XI.1989 (AMS). It was also flying at San Javier, Tucumán and La Viña, Catamarca the same day.

The southernmost record of this species is apparently an unusual, white female from Yacanto, Córdoba, no date (Breyer) (MLP). The Sierras de Córdoba have a dilute *yungas* element.

"Group E" *Tatochila* (the "*xanthodice* group")

Although this group contains only two species, they are united only by genitalic morphology. Their wing patterns, biogeography, and host plants are different enough to raise serious doubts as to their true affinity, and the morphology of the early stages is also somewhat equivocal.

Tatochila distincta Jörgensen (Fig. 17C, D)

The La Plata collection contains two Jörgensen specimens: ♂, Cerro Ensenada (Catamarca), 22.II.1915 (#2651) and ♀, Cerro Negro, same date (no number). These were selected in 1971 by L.E. Peña as "hololectotipo" and "allolectotipo" respectively, and so labeled. Both are small and dark.

Not uncommon between 3000–4000 m in dissected *puna*, and in the Quichua District including the *Sierras Pampeanas*, flying with *T. inversa* and *T. m. macrodice*. The life-history of this species has been published (Shapiro 1986d). It is apparently an *Astragalus*-feeder (Leguminosae) in nature, but can be reared on Crucifers. There are phenotypic differences between the Salta and Jujuy populations on one hand and the (topotypical) material from the *Sierras Pampeanas* (Cumbres Calchaquíes — Aconquija), which may ultimately justify naming subspecies within Argentina. Sexual dimorphism is somewhat reduced in this species.

2♂ 20 km N Humahuaca, Salta, 3700 m, 12.I.1978 (RE)
8♂ 3♀ Tres Cruces, Jujuy, 3800 m, 23.I.1986 (AMS)
1♂ 1♀ Abra Infiernillo, Tucumán, 20.I.1986 (AMS)
2♀ Cerro Zapallar, Salta, 3720 m, 22.I.1986 (AMS)

Genus *Hypsochila* Ureta (Figs. 18, 19; ranges 10B, 11B)

In early stages as well as adults, one group of species of *Hypsochila* appears to be the sister-group of the *Tatochila mercedis* and *autodice* (Crucifer-feeding) complexes. Unfortunately, the genus *Hypsochila* itself is in some disarray despite work by Ureta (1955, 1963) and a revision by Field and Herrera (1977). The latter was regarded by its authors as very preliminary, and was based largely on Herrera's Chilean material. The species limits were poorly defined, and the authors went so far as to state (p. 5): "Five of the six species. . . are very closely related and could be considered subspecies of a single widely distributed species. However. . . two of these species are known to fly at

the same time in at least two of the same localities..." The data reported here demonstrate that Field and Herrera were wise in continuing to treat these taxa as species, though tantalizing ambiguities remain. The Argentine species appear to fall into two groups, based on both adult and immature characters. Because the type-species is *H. wagenknechti* Ureta, the group to which it belongs (comprising in addition the taxa *sulfurodice* Ureta and *galactodice* Ureta) will retain the generic name, should the genus be divided as seems likely. This group has close affinities to *Tatochila* as noted above. The other group, comprising the taxa *argyrodice* Staudinger, *microdice* Blanchard and *huemul* Peña, has many unusual derived character states and is farther removed from *Tatochila*. All of its taxa are austral in distribution. No name is currently available for the group, should it be formally raised to subgeneric or generic status.

***Hypsochila argyrodice* (Fig. 18C)**

1♂ Cabo Peñas, Depto. Río Grande, Tierra del Fuego, 17.XII.1983 (ML)
1♂ Fitz Roy, Santa Cruz, loc. #26, 11.II.1979 (DE)

***Hypsochila microdice* (Fig. 18G, H)**

37♂ 11♀ Río Grande, Tierra del Fuego, 25.XI.1988 (AMS)
1♂ Estancia María Cristina, Route 3, Tierra del Fuego, 27.XI.1988 (AMS)
1♂ 1♀ Foot of Glaciar Martial, Cordón Martial above Ushuaia, T. del F., 29–30.XI.1988 (AMS)

These combined records demonstrate that the ranges of the two southernmost *Hypsochila* interdigitate and they cannot be conspecific. The Danish Expedition *argyrodice* from Fitz Roy appears to be the first mainland specimen with a precise locality. Breyer (1939) never saw it at all, even a specimen, but cites "Ushuaia, Röber." Hayward (1950, p. 92) records "Chubut" without data. I searched unsuccessfully for it in marginal weather at Fitz Roy on 20.XI.1988. *H. microdice* is abundant at Río Grande and its life-history is in preparation. The phenotype is quite variable, but not easily confused with anything else in the region. The two Cordón Martial specimens are large, especially the male, but still smaller than *argyrodice*. *Microdice* is a Legume-feeder and given the very close morphological affinities, the others are likely to be as well. I have no new data to report on *H. huemul*.

***Hypsochila galactodice* (Fig. 18D, E; 19C, F, G, H)**

1♀ Río Agrio, Neuquén, 10.IV.1932 (MLP)
2♂ Huacalera, N end Cerro Amarillo, 3250 m, Jujuy, 4.I.1980 (RE) (*)
1♂ Cordón del Viento, Neuquén, 3000 m, 28.I.1985 (AMS) (*)
2♀ Lago Meliquina, Neuquén, loc. #10, 12.XI.1979 (DE)

1♂ 1♀ Aluminé, Neuquén, 15–16.I.1981 (AMS)
1♂ Junín de los Andes, Neuquén, 13.XI.1988 (AMS)
1♀ Loncopué, Neuquén, 8.XI.1988 (AMS) (*)
1♂ 6♀ San Carlos de Bariloche, Río Negro, 15.XI.1988 (AMS)
13♂ 4♀ Esquel, Chubut, 17.XI.1988 (AMS)
(plus reared diapaused and non-diapaused material from Bariloche and Esquel)

Hypsochila wagenknechti wagenknechti **(Figs. 18I, 19A, D)**

6♂ 2♀ Las Cuevas, Mendoza, 31.X–1.XI.1988 (AMS)
21♂ 11♀ Arroyo de Agua Negra, above 3200 m, San Juan, 3.XI.1988 (AMS)

Hypsochila wagenknechti wagenknechti **"spring form"**

1♂ 1♀ Arroyo Chapelco Grande, 900 m, Neuquén, 15.XII.1979 (MG)
1♂ Chapelco, Neuquén, 1700 m, 24.II.1952 (S. Schajovskoy) (ML)

Hypsochila wagenknechti sulfurodice **(Fig. 18A, B, F)**

1♂ Huacalera, N end Cerro Amarillo, 3250 m, Jujuy, 4.I.1980 (RE)
3♂ Altos de Abra Muñano, 4165–4780 m, Salta, 21.I.1983 (AMS)
8♂ Tres Cruces, 3800 m, Jujuy, 7.II.1984 (AMS)

This group of taxa is so difficult that some critical determinations are provisional (marked *). The life-histories of *H. w. wagenknechti* and *H. galactodice* are fully known (Courtney and Shapiro 1986a, b; Shapiro, in preparation). They differ about as much as the adults: *wagenknechti* feeds in nature on Crucifers, *galactodice* on *Tropaeolum*. Brown (1987, p. 102) maps these two species as either allopatric or parapatric at roughly 32°S. Field and Herrera have *galactodice* only from Epulafquén, Neuquén on the Argentine side and *wagenknechti* only from Las Cuevas and the directly adjacent Quebrada de los Horcones, Mendoza — widely-separated localities, falling in the Western Patagonian District and the Cuyo District respectively. The Loncopué female and the male from Cordón del Viento, Neuquén are both virtually undeterminable, and both are geographically feasible as zones of primary (not secondary?) intergradation if these two taxa are biologically conspecific. To complicate matters, a second female *Hypsochila* taken the same day at Loncopué is quite different and does not agree with any described taxon.

The pair of apparent *galactodice* from Cerro Amarillo, Jujuy is extremely problematical. Although matching the description of *galactodice*, they differ from Patagonian specimens in exactly the same ways *sulfurodice* differs from nominate *wagenknechti*. If *H. galactodice* actually occurs some 2000 km N of its previously-known range, in a different biome and sympatrically with a subspecies of *wagenknechti*, there can be no question of conspecificity with that species. However,

the series is too short to rule out sampling error disguising continuous population variation at Cerro Amarillo, from a usual *sulfurodice* to a *galactodice*-like phenotype. My long series of *wagenknechti wagenknechti* from Mendoza and San Juan includes individuals which approach *galactodice* in phenotype, underscoring the variability of these animals and the potential unreliability of small samples. Unfortunately, females are rarely encountered and males are concentrated on relatively inaccessible hilltops, where they are difficult to catch. In the absence of *any* reliable, diagnostic morphological character this problem is insoluble at this time. Absolutely no tendency to resemble *galactodice* has been seen in any other *sulfurodice* (i.e. from localities other than Cerro Amarillo).

In the Cordón Chapelco near San Martín de los Andes a small, very dark form of (?)*wagenknechti* occurs in which the dorsal apical markings tend to fuse; the reflective gloss at the base of the wings is more pronounced; and the VHW pattern is extremely heavy. The pattern is vaguely suggestive of the next species. I am treating these as spring forms of *wagenknechti* because I have very similar specimens from Chile: Cumbres de La Parva, Prov. Santiago, 24.XI.1982 and Los Libertadores, Prov. Los Andes, 3900 m, 27–28.I.1983 (all AMS), taken right at melting snow-line in an area (just across the Paso Bermejo from Las Cuevas) where no other taxon is at issue. However, seemingly typical *galactodice* occurs at Junín de los Andes (first brood, XI.13), quite close to but lower than the Cordón Chapelco.

Near Las Leñas in southern Mendoza, 3♂ *Hypsochila* were collected on an altitudinal transect up Cerro de los Fosiles, 3.XII.1989: a typical *galactodice* at 2100 m, an intermediate specimen at about 3000 m and a typical *wagenknechti* at 3300 m. All are figured on Plate IV. Again, this suggests altitudinal stratification and intergradation (but the sample size is very small). Strikingly, the two higher specimens were hilltopping while the low-altitude one was visiting a dandelion on a *vega*, behaving much as a *galactodice* "should."

Problematic specimens of this group of taxa, including a striking aberration of *wagenknechti*, are shown in Figs. 18–19.

Hypsochila penai Ureta

So far known only from Chile. A ♂ in ML is labeled "Alto de Puripica, 4600 m." The country is not given. This locality is in Chile (22°30′S, 68°07′W) quite close to the Argentine border.

Genus *Phulia* Herrich-Schaeffer (Fig. 20; ranges 10C, 11C)

This is a classically high-Andean genus, restricted to *puna* and *altiplano* from C Peru through Bolivia to NE Chile and NW Argentina. All the Argentine populations known are treated by Field and Herrera (1977) under the name *P. nymphula* Blanchard. Genetically and ecologically these populations are somewhat diversified. Life-history and

electrophoretic data will be published (Shapiro, Courtney, Descimon & Geiger, in preparation).

In Argentina "*P. nymphula*" is distributed in four geographic regions. Rather than multiply names, I present representative data and discuss the status of available names potentially applicable to these populations.

(i) The *puna* of Jujuy and Salta

26♂ 13♀ Tres Cruces, Esquinas Blancas, Jujuy, 7.II.1984 (AMS), 23.I.1986 (AMS)

2♂ Abra de Pives, 4200 m, Jujuy, 29.I.1969 (ML)

1♂ near Turilari, Jujuy, 4000 m, 5.IX.1968 (ML)

1♀ Rosario de Coyahuayma, Salta, 4400 m, 11.IX.1968 (ML)

1♂ Río Cincel, Jujuy, 3800 m, 3.IX.1968 (ML)

Plate I. Pierid habitats in montane northwestern Argentina. A, view of *puna* dominated by *tola*, looking N from a summit near Abra Muñano, Salta; habitat of *Hypsochila wagenknechti sulfurodice*. ii.1983. B, Dissected *puna* at the head of the Quebrada de Humahuaca, Jujuy, near Abra Azul Pampa. Habitat of *H. w. sulfurodice*, *Tatochila distincta*, *T. mercedis macrodice*, *Phulia nymphula*, and *Colias blameyi*. ii.1985. C, *Yungas* in Salta, below Valle Encantado, showing deeply dissected topography. Habitat of *Tatochila orthodice* and *stigmadice* and *Teriocolias riojana*. i.1986. D, Valle Encantado, Salta, in the uppermost *yungas*, at the height of wet season; *Colias blameyi*, *Tatochila orthodice*, *T. stigmadice*, *Teriocolias riojana*. i.1986. E, Rocky summit in the Cumbres Calchaquíes, Tucumán (quichuan vegetation with large *Azorella* in foreground). Habitat of *Tatochila inversa*, *distincta*, *mercedis macrodice*, and *Colias blameyi*. i.1986. F, Dry subalpine shrub-steppe above Amaichá del Valle, Tucumán, looking toward the Valles Calchaquíes. This belt forms the apparent barrier between *Tatochila mercedis macrodice* above and *T. m. vanvolxemii* below. i.1986. All photos by AMS.

Plate II. Pierid habitats in montane west-central Argentina. A, *prepuna* with columnar cacti near Cachi, Salta. No endemic Pierid fauna, but *Tatochila autodice* and (seasonally) *Ascia monuste automate* common. i.1986. B, Riparian vegetation in wet season in the *monte*, Valles Calchaquíes between Fuerte Quemado and Cachi. *Tatochila mercedis vanvolxemii* occurs in similar vegetation farther S but is not known N of Amaichá del Valle at this time. i.1986. C, Precordillera near Potrerillos, Mendoza. *T. m. vanvolxemii* with possible introgression from *T. m. mercedis* are abundant here. x.1988. D, *Vega* at the head of the Arroyo de Agua Negra, San Juan, near the Chilean border. The only known locality for *Colias flaveola* in Argentina. Nearby occur *Hypsochila w. wagenknechti*, *Phulia nymphula* and other characteristic cordilleran taxa. xi.1988. E, Sparse alpine steppe in the Aconcagua Provincial Park, Mendoza, in early spring; *Phulia nymphula* very abundant. xi.1988. F, Rockslides among the summits overlooking the Paso Bermejo, Mendoza. *Hypsochila w. wagenknechti* abundant. xi.1988. All photos by AMS.


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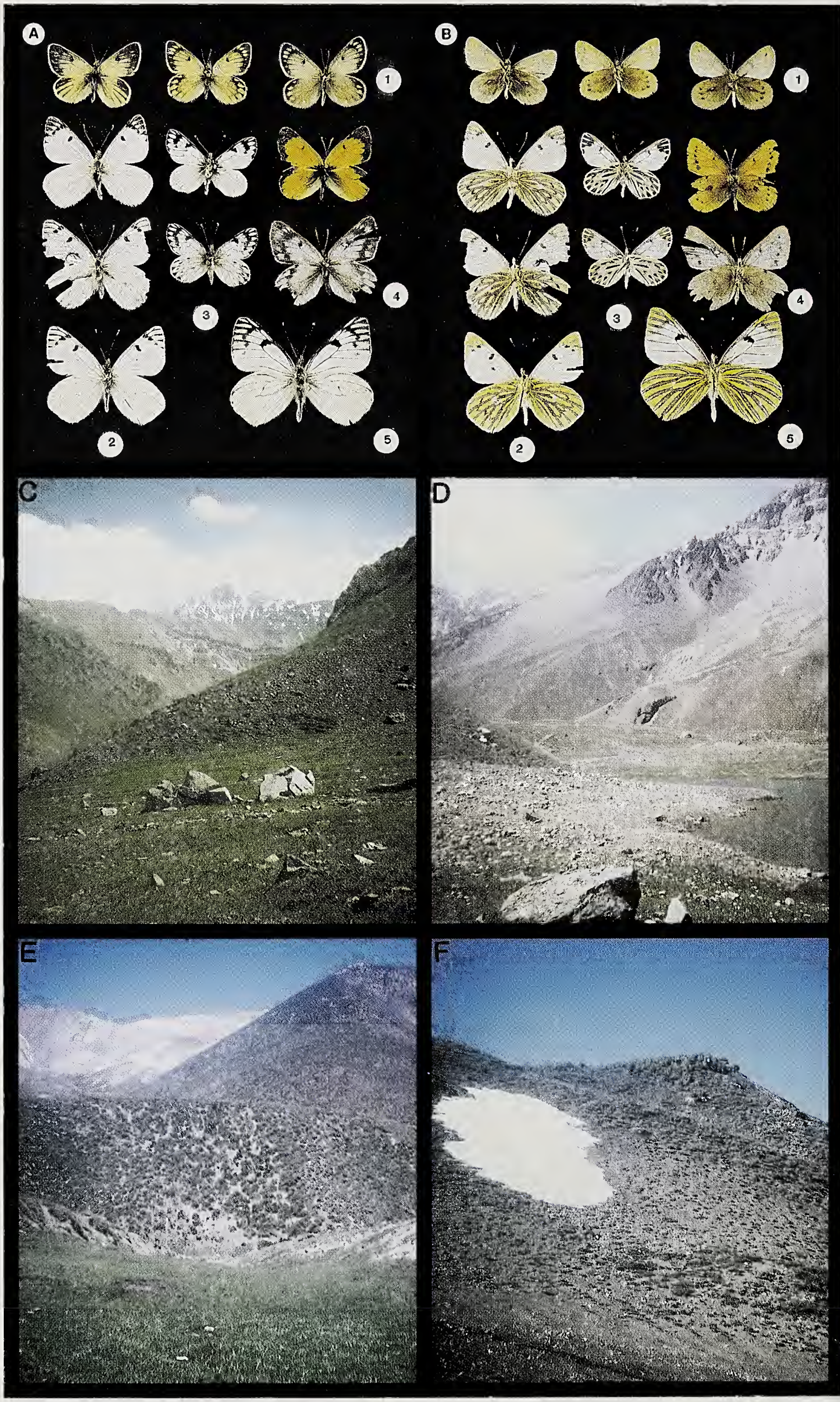
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Plate III. Pierid habitats in southern Argentina. A, partially inundated *mallines* at Loncopué, Neuquén, site of a hybrid *Tatochila mercedis sterodice* X *vanvolxemii* population. Also occurring here are *T. theodice*, *Hypsochila galactodice*, *Colias vauthieri*, and various other Patagonian taxa near or at their N limits. xi.1988. B, Mosaic of *Nothofagus* forest, subalpine steppe, and Patagonian grassland/ *mallín* E of San Martín de los Andes, Neuquén, a major ecotone. Hybrid *Tatochila mercedis mercedis* X *T. m. sterodice* with slight *T. m. vanvolxemii* influence eastward common in the valley; *Hypsochila ?wagenknechti* occurs above tree line and *H. ?galactodice* in the valley at nearby Junín de los Andes. *Eroessa chiliensis* and *Mathania leucothea* fly further west in the Valdivian forest. xi.1988. C, Shrub-steppe with a few small *Nothofagus* near San Carlos de Bariloche, Río Negro, in the deforested steppe-forest ecotonal zone. Now dominated by *neneo* (*Mulinum*, Umbelliferae). *Tropaeolum polyphyllum* abundant. This is the habitat of *Tatochila autodice autodice* X *T. a. blanchardii* intergrades and of *Hypsochila galactodice*. xi.1988. D, Patagonian shrub-steppe at Fitz Roy, Santa Cruz, the only definite mainland locality for *Hypsochila argyrodice*. xi.1988. E, Windswept bunchgrass steppe in the Department of Río Grande, Tierra del Fuego; habitat of *Hypsochila microdice* and *Tatochila theodice* near *staudingeri*. xi.1988. F, alpine shrub-steppe and *Nothofagus krummholz* in the Cordón Martial, Tierra del Fuego. *Hypsochila microdice* and a dwarf race of *Yramea cytheris* (Nymphalidae) occur here. xii.1988. All photos by AMS.

Plate IV. Zoogeographically important Argentine Pieridae and some of their habitats. A, upper and B, lower surfaces: 1. *Colias mendozina*, Aconcagua Provincial Park, Quebrada de los Horcones, Mendoza (across top: left, male, 30.XI.1989; center, yellow female and right, whitish female, 15.XII.1989). 2. Male *Hypsochila* from vicinity of Las Lenas, Mendoza, 3.XII.1989, showing apparent intergradation from *wagenknechti* to *galactodice* phenotypes. The two upper specimens are from >3000 m on Cerro de los Fosiles; the lower one is from a wet *vega* at 2100 m. 3. *Phulia nymphula* from the southernmost locality known in the main Andean cordillera, male (above) and female; Cerro de los Fosiles, near Las Leñas, Mendoza, 3100 m, 3.XII.1989. 4. *Colias vauthierii* from the northernmost known locality, Arroyo El Deshecho, near Las Lenas, Mendoza, 2100 m, 5.XII.1989, male (above) and female. 5. Male *Tatochila inversa*, Abra Infiernillo, Tucuman, 26.XI.1989, the only ♂ specimen of the first brood known to me. C, D, Habitats of *Colias mendozina* in Quebrada de los Horcones, Aconcagua Provincial Park, Mendoza. *Phulia nymphula* and *Hypsochila wagenknechti wagenknechti* also fly here; 3300–3900 m. XII.1989. E, Habitat of *Hypsochila* near *galactodice*, near Las Lenas, Mendoza, 3000 m, XII.1989. F, Alpine steppe near summit of Cerro de los Fosiles, near Las Leñas, Mendoza, 3400 m, habitat of *Hypsochila* near *wagenknechti* and of *Phulia nymphula*. XII.1989. (Figs. A and B by S. W. Woo; remainder by AMS.)

1♂ Tolar Grande, Salta, 3525 m, 15.I.1978 (M. Vargas) (ML)

(ii) The Quichua District

(a) Salta highlands

3♂ Cerro Zapallar, Salta, 28.XI.1989 (AMS)

(b) The *Sierras Pampeanas*

2♀ El Manchal, Catamarca, 4000 m, I.1959 (ML)

1♀ Cerro Muñoz, Tucumán, 4000 m, I.1959 (ML)

1♂ Summit above Abra Infiernillo, 3450 m, 26.XI.1989 (AMS)

6♂ 5♀ Huaca Huasi, Tucumán, 4150–4250 m, 2.III.1977, 4.IV.1977, 14.VII.1977, 1.IX.1978, 23.IX.1978, 28.IX.1978 (all S. Halloy and E. Domínguez) (ML)

(iii) The Cuyo District

25♂ 5♀ + 1 mosaic gynandromorph (Fig. 21), Las Cuevas to Puente del Inca, Mendoza, 31.X–1.XI.1988 (AMS)

16♂ 20♀ Arroyo de Agua Negra, San Juan, above 3200 m, 3.XI.1988 (AMS)

+ 28 additional specimens from the Paso Bermejo, Mendoza (MR, ML, BM, AMS)

4♂ 1♀ Cerro de los Fosiles, 3100 m, near Las Leñas, Mendoza, 3.XII.1989 (AMS)

3♂ Cerro de los Fosiles, 3300–3400 m, Mendoza, 3.XII.1989 (AMS)

(iv) The Cordón del Viento

1♂ Cordón del Viento, Neuquén, 3700 m, 28.I.1985 (AMS)

The Problem of *Phulia aconquijae* Jörgensen

Since its original description (1916), *Phulia aconquijae* has generally been synonymized to *nymphula* — beginning with Breyer (1939), who used it in a subspecific sense. Field and Herrera (1977) state that "a study of the original description and of topotypes show that this name is a junior synonym of *Phulia nymphula nymphula*." In taxonomy as in jurisprudence, however, the reasoning leading to a conclusion of fact must be spelled out before the conclusion can be accepted, and in this case it was not. Field and Herrera were unable to locate any definite material from the type-series, but state that "Topotypes are present in the collection of the National Museum of Natural History...and indeed...may represent syntypes (although they are not so labeled). A lectotype designation is not needed at the present time." The reader cannot reconstruct how Field and Herrera dealt with the differences identified by Jörgensen between his "new" species and *P. nymphula.*

Jörgensen was an unusually meticulous observer, and the question of how he came to erect a synonym of the well-known, widely-distributed *P. nymphula* has never been addressed. The clue lies in the description. Jörgensen knew, or thought he knew, *P. nymphula* from Bolivia, and used it as a comparison in his diagnosis of *aconquijae*. Although he gives a very precise description of the wing phenotype, it is clear that for him *the* critical character was the venation. He says (1916, p. 517):

"This new species much resembles *P. nymphula* Stgr. from Bolivia, but distinguishes itself beyond differences of color and pattern principally in that the second radial vein (as in the genus *Andina* Stgr. = *Piercolias* Stgr., AMS) issues directly from the subcostal and not, as in the other species, united for a while with it (in one example of the female they are united a short distance)."

This makes no sense if one has learned only the Comstock-Needham system of naming the wing veins. But Jörgensen is using an antique terminology which employs some of the same names as Comstock-Needham *but for different veins*. The "second radial vein" as used here means our M_2, which is entirely free in *Piercolias* and in *P. nymphula* but anastomosed with R_{3+4+5} in *Phulia paranympha* Stgr. from Bolivia. The "subcostal" is not our Sc, but the combined radials. Thus we may infer that Jörgensen had Bolivian *paranympha* misidentified as *nymphula*, and concluded that his material — true *nymphula*, in fact — was different and new. The source of this confusion was traced by Breyer (1939) and echoed by Field and Herrera (1977) but only in reference to the name *Phulia reedi* Giacomelli (1918). Giacomelli's type series was from Las Cuevas in the Paso Bermejo, Mendoza, that most accessible of high-cordilleran sites. Staudinger (1894) had misidentified Chilean material as his own *paranympha*, when it was actually *nymphula*. Giacomelli reasoned that his material from Mendoza was not *paranympha*, hence had to be something new! In 1924 Röber proposed the replacement name *joergenseni* for the Bolivian insect, if in fact Jörgensen's insect *aconquijae* were synonymous with *nymphula* (type locality Coquimbo, Chile): after all, wouldn't that leave the Bolivian species nameless?

In fact, *aconquijae*, that is, *Phulia* from the *Sierras Pampeanas*, like some of the sympatric *Tatochila* is perhaps marginally taxonomically recognizable on the basis of the very small size of September–October material, electrophoretic and early-stage characters. The populations in areas i–iii all differ at this (subspecific) level, but adult wing phenotyes are extraordinarily variable in all of them. (The Cordón del Viento population is known only from my specimen and an independent collection by MG, which I have not seen.) If it is ultimately desirable to name these, *nymphula* is the correct name for the Cuyo District populations, *aconquijae* remains available for the Calchaquíes-Aconquija animal, *reedi* is unambiguously a synonym of *nymphula sensu stricto*, and there is no name available (unambiguously) for the *puna* populations.

Field and Herrera present the type-locality information for *aconquijae* in a confusing way. On p. 19 they quote Jörgensen's list of localities (from his p. 517; Cerro Medio through Cerro Negro) without mentioning La Ollada, which Jörgensen finally refers to 16 lines later. Their list of material examined (p. 20) includes among localities *only* La Ollada as possible topotypes, as referred to in the text. Breyer (1939, p. 46) refers to Jörgensen's "types": "Ein Vergleich unserer Tiere

mit der Typen Joergensens..." Breyer's collection is at La Plata, where there are five Jörgensen *Phulia*, none identified as the type of *aconquijae*. They are in drawer 83 of the "Petrowsky collection" cabinet and are not listed as types in the type file. All have Jörgensen MS labels and they are from: Cerro Medio, 2♂ 1♀, 13.II.1915 and La Ollada, 1♂ 28.III.1916, 1♀ 17.III.1916. In MR are several more Jörgensen specimens bearing MS labels "*aconquijae n. sp.*" and "La Ollada/Catamarca," almost certainly syntypes. All of these are normal *Phulia nymphula* from the *Sierras Pampeanas*, not a new species.

Jörgensen himself notes variation in his venation character. The venation of several *Phulia sensu lato* appears quite labile. Very small *P. nymphula*, such as occur at Huaca Huasi in September, may have R_{3+4+5} crowded at the very apex of the FW, where it diverges from M_1, looking like it is about to be pushed off the apex altogether. This in fact has happened in *Infraphulia madeleinea* Field and Herrera from Peru, but Shapiro (1985) reported a female from the Department of Junín (above Lima) which had conserved the "lost" vein on both FW, and Lamas (*in litt.*, 15.XII.1986) reported a male from Pampa Galeras, Ayacucho with a 3-branched radial on one FW and 2-branched on the other.

The S extent of *P. nymphula* remains conjectural. The Cordón del Viento population, at 37°S (70°30'W), is considerably S of the farthest S record in the main *cordillera* (35°04'S). We have not found *P. nymphula* in seemingly suitable habitat in the Maule district, Chile (36°S, S.P. Courtney) or at Copahue, Argentina, above Chos Malal (37°45'), where *T. m. mercedis* leaks over on to the E slope.

Genus *Eroessa* Doubleday

Eroessa chiliensis Guérin

This remarkable species barely enters Argentina at the extreme W ends of the Nahuel Huapí (Río Negro) and Lanín (Neuquén) National Parks. Peña (1975) records it simply from Neuquén, but its potential habitats occupy less than 1% of the area of the Province. I have seen it between Puerto Blest and Laguna Frías in the Nahuel Huapí park. Jörgensen (1916) and Breyer (1936, 1939, 1945) were apparently unaware of its occurrence in Argentina and Hayward (1950) as usual cites only the Province, Neuquén. Schajovskoy, who was resident naturalist in the Lanín Park, knew it well and found it at Quechuquina (40°10'S, 71°35'W). MR contains a seemingly reared Schajovskoy male from there, dated 5.XI.1952. MLP has a male from San Martín de los Andes, Nqn., 27.I.1941 (R. P. Bilardi). The life history has been published (Angulo and Weigert 1974); Wagenknecht (1968) offered notes on the behavior and ecology of the adult. The host plant has been reported in print only by Peña (1975), who identifies it as *Flotovia* (= *Dasyphyllum*) *diacanthoides* Cabr., a Composite of the

primitive endemic tribe Mutiseae. It is a shrub or small tree, known locally as *Palo Santo*, and is typical of the Valdivian Tertiary relict rain forest (Ringuelet 1955) — one of the oddest hosts recorded for any Pierid in the world and thus seemingly underscoring the antiquity and taxonomic isolation of *Eroessa*.

Genus *Mathania* Oberthür

Mathania leucothea Molina

Another essentially Chilean species, in this case not restricted to the Valdivian forest but extending far north in *matorral* in the *precordillera*. In Argentina it occurs in the same areas as *Eroessa* but penetrates somewhat farther eastward — its range may have contracted as a result of 19th-century deforestation in the Lake District. Schajovskoy collected it frequently at Pucará in the Lanín National Park (5.XI.1958, 30.XI.1960, XII.1950, etc., MR) and I have seen it at Cerro Catedral near Bariloche as well as further W, and once in the hills just SW of the city limits. The hosts are mistletoes ("Quintral," *Phrygilanthus* = *Tristerix tetrandus* Ruíz and Pavón, Loranthaceae), which are common near Pucará. For aspects of its biology, see Courtney (1986).

Genus *Colias* Fabricius

Colias ponteni Wallengren = *C. imperialis* Butler

This biologically very important species remains "lost" since the original series was collected, and is discussed here because of the possibility it may yet turn up in Fuegia. G. Lamas writes (*in litt.*, 13.V.1981): "*Ponteni*'s type locality is 'Honolulu,' (collected by the Eugenies Expedition; a gross mistake), and the type locality of *imperialis* is 'Port Famine' (collected by P. King?). Port Famine is Puerto del Hambre, Magallanes, Chile (53°38′S, 70°56′W), which is S of Punta Arenas; the frigate 'Eugenies' was in Port Famine from 31.I to 2.II.1852, and *ponteni* was probably collected on an excursion the scientists aboard made to Mt. Tarn." Cerro Tarn (819 m) is right by the coast just S of Puerto Hambre. Apparently no one has seen *Colias ponteni* alive in over 137 years! Nor has anyone visited the presumptive type locality to look for it, though I have assiduously searched meadows with clover and vetch in various parts of Argentine Tierra del Fuego. Any Lepidopterist visiting the region should look for it. It is undoubtedly the morphologically most primitive *Colias* known, a living — or recently extinct — fossil (Petersen 1963, Berger 1986).

H. Descimon has raised (*in litt.*) the intriguing possibility that the Hawaii-Fuegia confusion arose over the South Sandwich Islands, one of the Falkland Islands Dependencies in the South Atlantic, — "Sandwich Islands" being an antique English name for Hawaii. These islands are so remote and isolated (latitude 56° to 59°S, longitude

26°15′W) and have such a harsh climate that the occurrence of any butterfly there would be extremely remarkable.

Colias vauthierii Guérin

This widespread and common Patagonian and Chilean species extends N into the transition zone between Patagonia and the Cuyo. Hovanitz (1970) claimed a new N record in agriculturalized *mallines* at Plottier in the valley of the Río Limay, Neuquén, 8.XII.1970. (There are no Plottier specimens in the Hovanitz collection at CAS: the only Argentine material is a series from "Coyaique," 14.I.1967, which could be either Coy Aike, Santa Cruz, or Coihaique in the pass between Santa Cruz and Aisén (Chile).) Breyer (1939) quotes Köhler for "Río Agrio" (p. 50). In Neuquén I have three N collections of this species: Aluminé (16.I.1981), Loncopué (8.XI.1988), and Chos Malal (28.I.1985). Loncopué is in the Río Agrio drainage.

Hayward (1973, p. 123) records this species from "Mendoza." Although no substantiating specimen has turned up, on 3.XII.1989 I found *C. vauthierii* common on *vegas* in the Valle de Las Leñas in southern Mendoza at 2100 m. This is a remarkable range extension which graphically illustrates the interdigitation of the high-Andean and Patagonian biota in the Cuyo. Two specimens from this population are shown on Pl. IV; they are completely "typical."

C. vauthierii and *C. lesbia* Fabr. co-occur at Chos Malal with no trace of interbreeding and apparently have a fluctuating zone of overlap across central Patagonia. Strays of *C. lesbia* occur regularly S to San Martín de los Andes, Neuquén and San Carlos de Bariloche, Río Negro and somewhat less often to Esquel, Chubut. *C. lesbia* is abundant in eastern Chubut (Trelew, Rawson, Puerto Madryn), breeding and perhaps overwintering at Comodoro Rivadavia since it has been taken there in spring.

Colias flaveola Blanchard (Fig. 22; range 10D, 11D)

Nominate *flaveola* has been considered a Chilean endemic, and no supposed subspecies are reported from Argentina. On 3.XI.1988 I collected 18♂ 4♀ *flaveola* above 3350 m in the Arroyo de Agua Negra, San Juan (30°12′S, 69°51′W) in typical habitat — high-altitude *vega* (sedgy stream bottom) (Pl. II–D). This locality is directly across the crest from the classic localities in the Province of Coquimbo, Chile. The Argentine material does not differ phenotypically from series from Baños del Toro, Coquimbo, 3800 m, 7.I.1972 (Hovanitz) and Río Seco, 11.III.1936 and 20.II.1937 (E. P. Reed) (all CAS). The Chilean skipper *Hylephila isonira mima* Evans (Hesperiidae) was taken in the Arroyo de Agua Negra the same day.

Colias mendozina Breyer (Plate IV; range Figs. 10D, 11D, 24)

Breyer (1939, p. 52) described this entity as *C. blameyi* f. *mendozina*. The text of his description follows: "Ist eine Abart, die sich durch starke Verbreitung der schmutzigen Gelbfärbung auszeichnet. Vorderflügel mit breitem schwarzen Apex und Aussenrand, von dem aus die breit geschwärzten Adern nach innen ziehen und mit dem Diskalfleck verfliessen. Wurzel hinten und Innenteil des Innenrandes intensiv schwarz. Hinterflügel am vorderen Tornus breit geschwärzt; Diskalpunkt rein gelb. Wurzel und Zellbasis tief schwartz. Unterseite zeichnungslos; Hinterflügel-Diskalfleck gelb und Wurzelfeld verdunkelt. — Typus und Paratypus in unserer Sammlung. — Habitat: Mendoza auf 3000 m Hohé, leg. Breyer." ("A variety, distinguished by the strong diffusion of the dirty yellow color. Forewing with broad black apex and outer border, from which the broad blackish veins reach inward and blend with the discal spot. Base and inner border intense black. Hindwing with front angle broadly blackened; discal spot pure yellow. Base of wing and cell deep black. Underside without pattern; hindwing discal spot yellow and basal portion darkened. — Type and paratype in our collection. — Habitat: Mendoza at 3000 m, leg. Breyer.")

The existence of this entity has been studiously ignored, e.g. by Berger (1986). On biogeographic grounds the occurrence of a "variety" or subspecies of *C. blameyi* Jörg. in the highlands of Mendoza seems unlikely, since the entire group to which that taxon belongs is tropical or subtropical except *C. flaveola*, which occurs S of the range of *blameyi* itself in Argentina and thus would apparently intervene between it and any putative subspecies in Mendoza. The description is barely adequate to allow one to visualize the animal. At the end of November 1989 I examined the three specimens of *mendozina* in the Breyer collection at MLP. The two types are faded and show evidence of having been mildewed. Both are labeled "Argentina Prov. Mendoza" and one bears a pink "TYPUS," the other a green "PARATIPUS" label. The third specimen is much brighter and fresher-looking, but has been broken and glued with a heavy, opaque material. It is labeled (in English) "Las Cuevas F.C.T. 15.I.1904/W.M.B. Seen also at Puente del Inca." F.C.T. presumably means "Ferrocarril Transandino." These specimens are clearly distinct from any other Andean *Colias* and not particularly close to *C. blameyi*. Only a few days after examining them I found *C. mendozina* flying in the Mendoza highlands! At present I have 9 specimens, all from Quebrada de Los Horcones (Lower Horcones to Confluencia), Parque Provincial Aconcagua: 1♂ 30.XI.1989 and 4♂ 4♀ 15.XII.1989, all AMS. A male and both color forms of the female are shown on Plate IV.

C. mendozina is easily told from other Andean *Colias* by its odd, almost mustard-yellow ground color (even the pale females are of a different hue than other Andean ones), small size, and short, almost

truncate, forewing. The dorsal black suffusion is weak and less extensive than in other taxa, scarcely more than in *C. flaveola*. The discal spot is large and rounded on males and variable on females. The large blackish area at the apex of the hindwing above and the brownish basal suffusion below are also distinctive. Oviposition was observed on a small, tufted, blue-flowered *Astragalus* (*arnottianus* (Gill.) Reiche) (det. R. Barneby).

The known localities for *C. mendozina* are on the so-called "normal route" used by climbers to access Cerro Aconcagua. Fig. 24 reproduces a map of the Parque Provincial with known habitats of appropriate type indicated, that is, *vegas*. I suspect *C. mendozina* will eventually be found on all such *vegas* up to at least 4000 m. Conversations with climbers and guides indicate many of them are familiar with the animal.

Whether *C. mendozina* will eventually be found outside the Aconcagua Park is highly doubtful. Although the vegetation along Highway 7 is commonly taken as typical of the montane *Cuyo* (e.g. Wingenroth and Suárez 1983), there is actually a rapid turnover in both floristics and community composition between the *C. flaveola* locality in San Juan and the vicinity of Las Leñas in southern Mendoza. *C. mendozina* could thus easily be a narrow endemic (like *C. flaveola*). Since it formerly and perhaps still could be found at Las Cuevas it should be looked for on *vegas* across the border in high-altitude Chile.

A formal redescription will be published at a later date.

The evolutionary and biogeographic history of this animal should be of great interest. If it is truly related to *C. blameyi*, it must represent an Interglacial stranding of an essentially tropical stock which managed to adapt to the strong temperate seasonality (including persistent snow for 5–7 months) of the Paso Bermejo. Its existence under our noses in the most accessible high-altitude locality in the Argentine Andes is a potent reminder of our extreme ignorance.

Colias blameyi **Jörgensen —** ***C. weberbaueri*** **Strand (Fig. 10D, 11D)**

MLP contains an original Jörgensen specimen — a female dated 13.II.1915 from Cerro Medio, as well as later topotypes (very dark ♂ and ♀, Cerro de la Mina, Depto. Tafí, Tucumán, IV.1933, no collector).

The life-history of this species has been described by Shapiro (1989b). Its distribution resembles the N part of that of *Phulia nymphula* or the high-altitude *Tatochilas* — *puna*, Quichua District and *Sierras Pampeanas*. Some representative data: Quebrada Carapunco, Abra Infiernillo, Pcia. Tucumán, 12♂ 3♀ 26.XI.1989, 35♂ 10♀ 20.I.86 (all AMS); Abra Molina, Cerro Zapallar, Salta, 18♂ 7♀ 28.XI.1989, 5♂ 7♀ 22.I.1986 (all AMS); 1♂ 2♀ Valle Encantado, Salta, 22.I.1986 (AMS); 13♂ 3♀ Esquinas Blancas, Jujuy, 7.II.1984 (AMS); 1♂ Abra Pampa, Jujuy, 7.II.1984 (AMS). The Abra Infiernillo and Abra Molina data

unambiguously indicate at least two, perhaps three broods, the first beginning immediately upon the onset of the rains (in November the *Astragalus* are just beginning to grow and bud).

Variation among populations is quite noticeable. All the Argentine material I have seen has at least traces of an androconial patch in the male, but material from the *puna* is colored more like Bolivian *C. weberbaueri* than is topotypical *blameyi* from the *Sierras Pampeanas*. CAS has long series of *weberbaueri*. In a group of 9♂ from "50 km S Oruro, 3700 m, 14.I.1972, W. Hovanitz," 7 have no androconial patch, 1 has traces, and 1 has a well-developed patch and is indistinguishable from Jujuy males. This site is roughly 475 km NNW of Abra Pampa. Further study will almost certainly demonstrate the conspecificity of these taxa. It is quite unusual to find such variation in a secondary sexual character and potentially of great evolutionary interest. Presence of androconia appears primitive relative to absence in *Colias*. This, however, does not necessarily imply S-to-N movement in the history of the green complex.

Genus *Eurema* Hübner

Eurema deva Doubleday

A common, weedy, highly dispersive species in N Argentina, reaching far S as strays in much the same manner as *E. lisa* Bdv. & LeC. in North America migrates N-ward in summer. My S-most records are Bariloche, Río Negro, 17.I.1984 and Caleta Olivia, Santa Cruz, 9.XII.1989. It also reaches high elevations, such as Abra Infiernillo, Tucumán, 3300 m, 20.I.1986. All of these were females.

Genus *Teriocolias* Röber

Teriocolias riojana Giacomelli

This altitudinal disperser apparently reaches the summits in the *Sierras Pampeanas* remarkably early in the rainy season, as single females were taken at Abra Infiernillo, 26.XI.1989 (Tucumán) and Cerro Zapallar, 28.XI.1989 (Salta) (both AMS). No known host plants were available in either site so early in the year.

Discussion

The raw data for an analysis of the zoogeography of the faunas and taxa reviewed here are based on collection records. Tables 1–2 present the species compositions of 25 selected faunas in Argentina and Chile. They are variably well-studied; richness is not pro-rated by area. Thus the term "Puna de Atacama" covers a vast and heterogeneous area — partly *puna* and partly cordilleran — which overall has been visited by perhaps ten collectors and is too poorly known to be subdivided yet, although it contains great riches and much endemism. Chos Malal,

Aluminé and Loncopué are dots on the map which have been visited by only one or two collectors, but frequently and are thus well-known. Much of the Argentine data used here is explicitly presented in the previous section. That which is not is based on precise and reliable sources, including the collections enumerated in the Acknowledgments, the author's collections at U.C. Davis (=AMS), and a handful of publications. By and large, the Argentine literature is much too vague and full of misidentifications to be credible for use in analytical biogeography. The Chilean data are from Herrera and Field 1959, Field and Herrera 1977, Herrera 1953 and 1970, and unpublished data provided by Herrera, S. P. Courtney, and AMS. Chilean biogeographic concepts are from Artigas (1975), Peña (1966), Davis (1986), Irwin and Schlinger (1986), and Hueck and Seibert (1972). Unsatisfactory as the data may be in scope and repeatability, they are far better than for any other part of the Andean region except for the Satyrid faunas studied by Michael Adams in Colombia and W. Heimlich in the Southern Cone.

Many indices of faunal similarity exist, which allow one to compare areas and to construct a hierarchical "classification," or dendrogram, of faunas based on shared elements (species, subspecies). Two recent reviews (Janson and Vegelius 1981, Hubálek 1982) have identified Sørensen's (1948) coefficient as one of the best if not the best in terms of objectivity and properties. (Although Sánchez and López-Ortega, 1988, disagree, their objections do not apply to these faunas.) From the values in Table 3 a dendrogram can be derived by cluster analysis (Fig. 23). This approach allows an easy visualization of overall faunal affinities, but its use for historical reconstruction is limited, as in all phenetic methods.

The dendrogram shows few surprises, but does offer some useful insights. It emphasizes the distinctness of the central-Andean high-altitude faunas of the N from the Patagonian faunas, at least at the taxonomic level used here. (The extremity would have been softened had subspecies not been weighted equally with full taxonomic species in the analysis.) The only northern fauna falling outside this cluster is the Valles Calchaquíes, the arid depression lying W of and in the rain shadow of the *Sierras Pampeanas*, which represents the N-most extremity of the *monte* both floristically and faunistically (Hayward 1955b) — its fauna is small and depauperate and quite similar to that of the Uspallata Valley (Precordillera Mendocina) in the Cuyo District; none of the highland entities, even the altitudinal migrants, descend into it. (If *Ascia monuste* had been counted, it would count as a regular migrant crossing both highlands and valleys, cf. Hayward 1931.) These two localities in turn cluster with the Gulf of San Jorge (Comodoro Rivadavia), which has the rarefied desertic fauna at the opposite end of the *monte*. The analysis does not include the *prepuna*, but its fauna is virtually identical to that of the Valles Calchaquíes. This fauna thus wraps around the seasonally arid lower reaches of all the highlands in

western Salta and Jujuy and in Catamarca and La Rioja.

Farther S, the N-Patagonian localities (Cordón del Viento, Loncopué, Aluminé, Bariloche, San Martín) cluster stair-step fashion. The sequence is reversed in the S because of the heavier Chilean influence at San Martín. This emphasizes that faunal turnover is not a simple function of distance from sources. In the Patagonian Andes the passes provide variably effective access for both low-altitude moisture and the Valdivian biota. From Bariloche south the Chilean contribution is less, not because the passes are more difficult but because the butterfly fauna becomes sparse in the very wet W-slope climates.

One of the more interesting clusters is of Chos Malal with the Chilean Central Valley; the latter has a conspicuously Patagonian element in the form of *Colias vauthierii* (and *Yramea cytheris*, etc.) not easily predictable from climatic data. This is explicable under the dispersal model of Caviedes and Iriarte (1989), discussed later.

In order to attempt reconstructions of specific histories, one need take into account the identities of individual taxa shared and not shared among faunas, the geographic distributions of individual taxa and the relationships of the ranges among related taxa, the degree of taxonomic differentiation and endemism in different regions, and the repeating patterns of distribution of different lineages, corresponding roughly to the "generalized tracks" of Croizat (1964; see also Craw 1982). Ultimately the phylogeny of the individual genera and of the Andean Pierini will be resolved, but so ambitious an undertaking must await much more data on "biology." Within the area covered by this study, however, patterns are already evident and in some cases their causation may be inferred. This returns us to the objectives enumerated in the Introduction.

The Uniqueness of the Puna. The high-altitude *puna* of NE Chile has a remarkably large and diverse fauna of Pierini, much of it endemic at the species level, which appears to dilute rapidly once one crosses the crest into Argentina. Far NW Argentina is very poorly collected due to its inaccessibility, difficult topography and harsh climate. Large areas are not only roadless but essentially uninhabited. To my knowledge no one has ever collected in the Sierra de Calalaste or farther W in N Catamarca, or even from Highways 27 or 17 in W Salta or from Highway 70/b in Jujuy. This is very bleak, barren terrain with many salt flats. The interesting Pierini are to be expected on bogs and rocky summits, not on the *tola*-covered flats through which most of the roads go. Thus, off-road vehicles or pack animals are required. When we do this work, I imagine we will extend the ranges of at least part of the Chilean *puna* fauna, perhaps including *Infraphulia ilyodes* Ureta, *Pierphulia rosea* Ureta, *Hypsochila penai, Tatochila mariae* Herrera, and *T. distincta fieldi* Herrera — just as the range of the genus *Hypsochila* will surely be extended into Bolivia, where there are no records today.

The very rich Chilean *puna* fauna is a S-ward extension of that of the Peruvian *altiplano* and seasonally dry high *Sierra*. The greatest faunal diversity of Andean Pierini is between the Peruvian Departments of Junín and Cusco, with perhaps the maximum diversity of *altiplano* taxa in Arequipa and of *Tatochila* in the complex ecogeography incorporating *yungas*, *jalca*="*páramo*" in the Peruvian sense (which is not the same as its use in Colombia, Venezuela and perhaps Ecuador), and *altiplano* within short (air) distances. These faunas appear to rarefy to the E in Bolivia, but collecting has been so spotty that little can really be said. Within the *puna* and *altiplano* the small Pierini (except perhaps *Phulia nymphula*) are restricted to bogs or bog margins at least in dry season (Shapiro 1985, 1986a, Shapiro and Courtney 1986). This limits their dispersal and seems to have promoted local differentiation and subspeciation. *Infraphulia madeleinea* females are very poor fliers — *I. ilyodes* are somewhat better — and electrophoretic as well as morphological data suggest that different allopatric populations of small pierines are evolving in isolation from one another. Despite seasonal variability, many of the bogs are certainly of Pleistocene age and, like Nearctic bogs supporting relict butterflies, have been able to sustain isolated populations for millenia. The bog illustrated by Weberbauer (1945, pl. XIII, p. 391) at Morococha (4500 m) has an exceptionally rich fauna and had not changed visibly in the 80-odd years since the picture was taken; pasturage does not appear harmful.

Phulia nymphula is the most ecologically versatile and dispersive of the small Pierini, in Peru (Pérez 1982, Lamas and Pérez 1983) as elsewhere; it is not surprising that it is so widely distributed in N Argentina (see below).

The Quichua District and the Sierras Pampeanas. There is great similarity between the high-altitude faunas of Salta and Jujuy and that of the Pampean Sierras (*Cumbres Calchaquíes — Sierra de Aconquija*) in Tucumán and Catamarca. The affinities of these high-altitude faunas, in turn, are with the *puna*. *Phulia nymphula* (*aconquijae*) is very instructive. In the *puna* above the Quebrada de Humahuaca, *P. nymphula* flies at the same elevation (albeit often in different habitats) as *Tatochila m. macrodice, T. d. distincta, T. inversa*, and *C. blameyi*. In the *Sierras Pampeanas* it occurs mostly above those species — mostly above 4000 m, though descending in autumn (March–April) as low as 3100 m (as noted by Jörgensen, 1916). It is not clear whether this altitudinal stratification in the *Sierras Pampeanas* reflects climatic differences or merely the occurrence of *Phulia* habitat — sandy alpine grassland-steppe with only very low plants — mainly above the *Tatochila* concentrations, which occur on rocky substrates below the glacial-pothole landscapes. As noted under that species, Pampean Sierra *P. nymphula* might be recognized as a subspecies. The same is true of *T. inversa*, *T. distincta* and perhaps even *T. m. macrodice*, and,

as noted above and in Shapiro (1989b), topotypical *Colias blameyi* seem to grade into *C. weberbaueri* both NW and N of the *Sierras Pampeanas* in the Quichua District. The distances are not great (100–150 km) between the highlands of Salta and Jujuy and the *Sierras Pampeanas*, but the ecological barriers are formidable. These barriers are traversed annually by *Ascia monuste automate* and perhaps by *Teriocolias*, as well as by many other seasonally migrant Lepidoptera. It seems unlikely that any of the true high-altitude Pierids are presently moving between the ranges. This might have been much easier in the Pleistocene. Halloy (1978, 82, 83) provides the most in-depth description and analysis of the Cumbres Calchaquíes from ecobiogeographic, physiological, and paleoclimatic perspectives. He finds that from a late Pleistocene glacial maximum, they are continuing to rewarm, and the snow line is still regressing upslope. If we know little of the regional biota before the Quaternary, we can still infer that the differences between populations in the *Sierras Pampeanas* and the main *cordillera* and *puna* are unlikely to antedate the later Quaternary. Using this inference, it may be possible to calibrate "molecular clocks" for the Andean Pierids more precisely than has been done heretofore. All these mountains attained alpine heights only in the Plio-Pleistocene. Are the insects conceivably any older?

It is very striking that the genus *Hypsochila* appears to be absent in the well-collected *Sierras Pampeanas*, eluding Giacomelli, Jörgensen, Hayward, Halloy, Domínguez, and me. *Hypsochila* is also unrecorded from Cerro Zapallar (Cuesta del Obispo). In fact, there are no records to connect up *H. w. wagenknechti* of the temperate cordillera of the Cuyo District with *H. w. sulfurodice* of the *puna* (San Antonio de los Cobres, Quebrada de Humahuaca). This is probably significant. It also casts doubt on the true conspecificity of the *galactodice*-like specimens from the *puna* and those from the main range of that entity far to the S in Patagonia. Indeed, it is by no means certain that *wagenknechti* and *sulfurodice* are conspecific. The zone where no *Hypsochila* occur is the zone of heaviest seasonal precipitation in the uplands, precisely where the tropical northeasterlies are wrung out at the head of the *yungas*. This may well be a limiting factor on *Hypsochila*, which is happy in the extreme aridity of the summits above Abra Muñano. It may also contribute to the upslope displacement of *Phulia* in the Cumbres Calchaquíes.

The seasonal presence of *Tatochila orthodice* and *stigmadice* in these same high-precipitation areas reinforces the impression that contemporary climate exerts strong control over contemporary distributions. These are true *yungas* species, which do occur in the wetter parts of the true *puna* close to the tops of the big canyons, without penetrating into *tolares*.

In summary: the wet alpine reaches of the *Sierras Pampeanas* share their fauna of *Tatochila* and *Colias* with the wetter parts of the Quichua District in Salta and Jujuy; the altitudinal distribution of

Phulia is somewhat skewed; and *Hypsochila* is absent from both, though common in the drier parts of the Quichua District and in the *puna*. These patterns were probably created in the late Pleistocene and are controlled today by micro- and mesoclimate distributions.

Connections Between the Cuyo *and the Quichua District and* Puna. The fauna of the high cordillera in Mendoza and San Juan is depauperate. I have not included *Colias mendozina* in the analysis only because it was rediscovered as this paper was about to go to press. It is the most unusual faunistic element in the Paso Bermejo but at present we cannot say whether it is more closely related to *C. blameyi* of the *puna* or to *C. flaveola*. (It is striking that if *C. blameyi*, *flaveola* and *mendozina* are combined, their range approximates that of *Phulia nymphula sensu lato* which, as noted previously, is differentiated into several segregates adapted to either tropical or temperate seasonality.) The only true *puna* element found in the alpine elevations of the *cuyo* is *Phulia nymphula*. *Hypsochila wagenknechti* is present as a presumptive sister-subspecies of the *puna sulfurodice*, and there may be either *T. m. mercedis* — *T. m. macrodice* hybrids or intergrades in San Juan. *Colias flaveola* seems limited to a very narrow latitudinal band on both sides of the Andes. Although Descimon (1986) treats it as potentially conspecific with *blameyi*, *weberbaueri*, etc., there is little reason to do so. Thus, the very rich *puna* Pierid fauna rarefies very rapidly once the regime of the tropical "Bolivian Winter" is replaced by the true cordilleran winter with a more or less continuous snow pack which forces a several-month interruption in butterfly activity. Since *Phulia nymphula* has adapted its life-cycle to the mendocino winter it is unclear what limits its range farther S, but it seems to drop out before the Maule district. *H. w. wagenknechti* continues S to Laguna del Maule and seems to segue into *H. galactodice* in NW Patagonia in a manner which remains unclear (see below). The *cordillera* was very heavily glaciated in the *cuyo*, and at present it cannot be told whether *P. nymphula* reinvaded from the NW after deglaciation or had been depressed to lower elevations, such as the *precordillera* above Uspallata, and reinvaded upslope.

The Las Leñas fauna (35°04′S, 70°02′W) is very unusual and interesting in presenting an altitudinally-stratified mix of northern and southern elements, including *P. nymphula* and *H. wagenknechti* above 3000 m and *H. galactodice* and *Colias vauthierii* below. The same phenomena are reproduced in the Lycaenid genus *Itylos* (Shapiro, unpublished data). The habitats of *P. nymphula* on Cerro de los Fosiles are very local and specialized in aspect and vegetation. One might expect a *puna* species to occur at ever-lower altitudes to its S limit outside the tropics, but the known *P. nymphula* sites on Cerro de los Fosiles are all higher than its lowest sites in the Paso Bermejo further N, and it is not a *vega* species as it often is in the Paso Bermejo. Indeed, its habitats

near Las Leñas are more like those where it has been taken in the Cordón del Viento.

The Cordilleran – Cordón del Viento Connection. This isolated, high, arid pre-Andean range, dominated by the 4710 m Volcán Domuyo, has the S-most known population of *Phulia nymphula* and also has a *Hypsochila*, unfortunately thus far known from only one male, which may be *galactodice* or *wagenknechti* or something inbetween. The distance to the nearest *Phulia* known in the *cordillera* is between 175 and 225 km. The presence of *Hypsochila* here is especially interesting in view of its absence from precordilleran ranges further N. Again, either these taxa were depressed to low elevations during the Pleistocene or colonized in the past 10–15,000 years. The distances involved imply the former as more likely, especially for *Phulia*. Thus, these high-altitude taxa may at one point have entered quite low parts of far NW Patagonia (the Payunia district), where we now find a mosaic of Patagonian and *monte* elements segregating by micro- and meso-habitat.

Geography of the Tatochila mercedis *complex.* It is quite clear that *T. m. macrodice* is the true central-Andean representative of this polytypic species, and most closely related to *T. m. arctodice* of the far N. In N Argentina as well as in Peru and Bolivia it has a remarkable ecological amplitude, occurring in both wet and very dry climates at high altitude. Its great vagility undoubtedly contributes to this, and it migrates elevationally with season in much of its range. Both it and *arctodice* are adapted to tropical seasonality, and its absence from the *cordillera* in the Cuyo District (despite the queried Mendoza record, not in Hayward 1950) is consistent with this: it has no place to go in winter and (in the laboratory) does not seem to be able to diapause. Diapause was, however, evolved as the complex invaded the temperate climates of the Southern Cone. The non-diapausing *macrodice* comes spatially very close to *T. m. vanvolxemii*, which diapauses in winter, along Highway 307 between Abra Infiernillo and Amaichá, but no actual contact has been found and the two are separated by a zone in which neither seems to occur.

Otherwise, *T. m. vanvolxemii* contacts and exchanges genes with *T. m. sterodice* and *T. m. sterodice – mercedis* hybrid populations along the W and SW edges of its range in Neuquén and Río Negro; its populations in the Mendoza *precordillera* (e.g., Potrerillos) and below Copahue and W of Chos Malal show signs of past or perhaps present introgression from *m. mercedis*, though the populations at both Mendoza and Chos Malal themselves appear pure; and the population in the Gulf of San Jorge warm pocket (Comodoro Rivadavia) presents a normal summer *vanvolxemii* phenotype but its cold-season brood displays strong *sterodice* influence. Intergrading populations in the San

Jorge District are clearly dependent on local populations of adventive Cruciferous weeds and cannot be very old — indeed, their ruderal character argues that the intergradation itself is likely to be secondary, and of recent origin.

True *T. m. mercedis* enters Argentina from Chile in NW Patagonia, but it does not seem to occur anywhere where it does not contact and hybridize with *T. m. sterodice*. Its range in Chile is basically limited to the Mediterranean climate belt, from Copiapó to Valdivia, and it does not occur in the "pampas" of NE — C Chile or approach *T. m. macrodice* closely anywhere except perhaps in Coquimbo and San Juan. The oldest museum specimens of *T. m. mercedis* from NW Patagonia date from 1939, with intergrades already present — so the phenomenon has a minimum age of some 50 yr, or 150 generations, but deforestation and land-use patterns suggest it could be at least twice that age if it in fact is a recent, man-influenced phenomenon.

Of all the Argentine Pierids, this complex most accurately mirrors the phytogeography. It also has the most extensive distribution of any Pierid, and probably any butterfly, on the continent — from central Colombia to Ushuaia, though avoiding forested and lowland-tropical habitats.

The Relationships of Fuegia and their Evolutionary Implications. Although Fuegia is recognized as a separate phytogeographic entity, its butterfly fauna is less distinct than heretofore supposed — though it has more Pierid taxa than the Cuyo District! The allegedly endemic *Tatochila* and *Hypsochila* are either also found on the mainland (*argyrodice*, *microdice*) or are clinal, with no sharp step at the Straits of Magellan (*theodice* ssp., *sterodice/fueguensis*). These facts argue against postglacial higher sea levels as responsible for isolation and differentiation-by-vicariance in the far S. But interesting evolutionary problems remain.

The Quaternary history of Tierra del Fuego is exceptionally well-known (Auer 1956, 1958, 1965, 1966, 1970). All of the mountains were glaciated; glacial retreat began some 16,000 BP. The entire vegetation of Fuegia can be assumed to have developed in this period, and it is not surprising that only 3% of the Fuegian flora of 545 vascular plant taxa is endemic; some 64% of the flora occurs N up the Andes on both slopes, 2% only on the drier Argentine side, 4% only in Patagonia E of the Andes and 8% N in Chile only (Moore 1983). The Fuegian Pierid fauna is overwhelmingly a steppe fauna; all the species occur on the Patagonian mainland in steppe, though two (*Tatochila theodice* and *T. sterodice*) also occur in the subhumid Patagonian Andes. *T. t. theodice* is recorded in Chile S to Victoria, at about the same latitude as Aluminé, but the species apparently continues S along the E slope of the Andes, grading into ssp. *gymnodice* and thence into ssp. *staudingeri* in Fuegia. The type locality of *gymnodice* is Punta Arenas, Magallanes, which further confuses the situation! *T. m. sterodice* is not

recorded unambiguously in Chile at all, though again the Magallanes populations are part of a cline between it and *fueguensis*. None of this should be surprising, were the 10,000-yr-old Straits of Magellan not taken unduly seriously as a barrier. Moore (*op. cit.*, p. 33) says: "The four principal climatic and vegetation zones described in passing from N and E to S and W Fuegia. . .parallel rather closely the sequence seen N of the Estrecho de Magallanes in traversing cool temperate Argentina and Chile from the Atlantic to the Pacific Oceans. Since all plant species can only occupy areas with climatic and ecological conditions within their range of tolerance it is not surprising that some species restricted to the drier steppe areas of NE Tierra del Fuego extend N-wards in the drier parts E of the Andes. . ." The only question is whether the Pierids crossed into Tierra del Fuego before or after there was a water barrier. In any case, the taxa are both weak and young and the climate unstable (Markgraf 1985).

More interesting is the hostplant specialization of those taxa. All three subspecies of *Tatochila theodice* feed on Legumes. So does *Hypsochila microdice* (and probably also *H. argyrodice* and *H. huemul*, which seem very closely related). How are we to interpret this oddity in a Crucifer-feeding lineage? Of all *Tatochila*, *distincta* is closest to *Hypsochila* in genitalia (Field 1938, Herrera and Field 1959, Field and Ferrera 1970). This has not been resolved electrophoretically (Shapiro and Geiger, unpublished). If they were sister-taxa, one could then treat Legume-feeding as a symplesiomorphy, and Crucifer-*Tropaeolum* feeding would then have arisen independently in both lineages, and represent convergence. But this is very improbable. The fact that most pierines globally feed on mustard-oil-containing plants argues against it. So does the remarkably close resemblance of the early stages of the Crucifer-*Tropaeolum* feeding branch of *Hypsochila*, which includes *galactodice* and *wagenknenchti*, to the Crucifer-feeding *Tatochila* of the *autodice* and *mercedis* complexes. (*T. theodice* is highly divergent in its early stages, and its affinities may actually lie with the *orthodice-stigmadice* end of the genus, a notion supported by certain pattern characters and wing pigments of the adults, and karyotypes (deLesse, 1967; Shapiro, unpublished).) If Crucifer-feeding is the symplesiomorphy, Legume-feeding has originated separately as a derivative condition in both genera. It is not clear whether it arose in sympatry, however, Legume-feeding may have arisen more than once — perhaps three times — in *Tatochila*. These conundrums can be resolved only when the entire group of genera can be subjected to a thorough cladistic analysis incorporating early-stage data.

Some Legume-feeders have austral distributions. If they were derived from more northerly Crucifer-feeders this makes sense: although Crucifers extend at least as far S in Fuegia as Legumes and are actually more numerous, their distribution is very patchy and their biomass is much less than that of small vetches on the steppe. (Introduced weedy Crucifers are now extremely abundant around towns, but this is a

recent condition.) Herrera and Covarrubias (1983) claim that the Andean-Patagonian Pierini are of Gondwanaland origin, however — suggesting that Legume-feeding (discovered since 1983) would represent the primitive condition. Is there any independent support for the Gondwanaland claim? The only suggestive datum is the bizarre provenance of *Colias ponteni.*

Biogeographers have failed to reach consensus over the interpretation of "centers of origin," a fact which has exposed the entire field to ridicule (Cain 1944, Croizat *et al.* 1974). The location of an endemic primitive taxon is not a reliable indicator of a center of origin, because primitive forms often survive in isolated regions far from where they originated (supposedly because of a lack of competitors). Any biogeography text gives several examples, the Tuatara (*Sphenodon*) being one of the commonest citations.[4] *Colias ponteni* is, genitalically, easily the most primitive living (or recently extinct?) member of its large genus. (It was classified by Peterson, 1963 in its own genus, *Protocolias.*) Is its inferred endemism in Tierra del Fuego an indicator that the entire genus is of Gondwanaland origin? Its nearest relative seems to be *vauthierii*, which occurs in Patagonia and the Central Valley of Chile. Electrophoretically all the South American *Colias* seem to cluster together, including *vauthierii* (Descimon and Geiger, pers. comm.). There is no indication in these data that *vauthierii* is the stem-species of the monophyletic Andean group inferred by Descimon (1986), or the group's sister-taxon. Nor do the global data on *Colias* support a Gondwanaland origin for the genus: the only other austral *Colias*, *C. electo* L., has a spotty relict distribution in east, central and southern Africa and belongs to a Palearctic species-group.

The Limits of Patagonia. The traditional political limit of Patagonia is the Río Negro, but there has never been a formal jurisdiction named "Patagonia" and in any case the biota on one bank of the Río Negro does not differ from that on the other. The Argentine phytogeographical literature attempts to define boundaries in the low, undulating relief of N Patagonia where it contacts and intergrades to the *monte* and *pampa* (Morello 1958, Ragonese and Piccinini 1969). From a pierid standpoint, Patagonia extends into the river bottoms of NW Neuquén (the Payunia district) which form the N limits of *Colias vauthierii* and some

[4] This concept was articulated at least as early as 1752 by Maupertuis, who wrote with reference to the alleged occurrence of "giants" in Patagonia (Tehuelches or Ona) and "dwarves" in the north-polar regions (Eskimos): "If there is truth in what the travelers tell us of the Strait of Magellan and the lands of the far North, the races of giants and dwarves settled there because of the fitness of the climate or, what is more likely, because. . .they were driven to those regions by other men, who feared the giants or scorned the pygmies. . ." (*Origine des Animaux*, p. 266) Although the Patagonian giants were ultimately debunked (Adams 1962), the existence of *Colias ponteni* in the fairly recent past is supported by a handful of specimens.

Lycaenids and Hesperiids as well, and form part of the *Tatochila mercedis-sterodice-vanvolxemii* intergradation zone. In the reciprocal sense, the *monte* and *pampa* penetrate Patagonia as far as the genetic influence of *T. m. vanvolxemii* extends, i.e. the Gulf of San Jorge. The S limits of *Colias lesbia* (as an occasional seasonal breeder) and *Eurema deva* (as an immigrant) are in the same area. It would be instructive to use Satyrids to define the limits in these same areas, as they are grassland-associated while the Pierids are not necessarily so.

Quaternary Climate Dynamics and Dispersal Routes. During the Quaternary the extreme aridity which characterizes the coastal deserts of Peru and northern Chile developed, serving as a very effective barrier to contain the biota of the Andean highlands. At the same time, there is reason to believe that precipitation waxed and waned repeatedly in temperate Chile, resulting in pulsations of N-ward migration by the Valdivian rain forest. Relict elements of that forest exist today in such areas as Fray Jorge, Talinay and Mantagua in Coquimbo at roughly 30°S, near the N limits of many organisms of central Chile including the butterflies *Tatochila mercedis* and *Colias vauthierii*. The best butterfly indicator of the Valdivian forest, *Eroessa chiliensis*, seems to stop at about 35°S (Constitución). Caviedes (1990) provided a predictive model of precipitation which generates up to 9-fold increases in rainfall in central Chile with T depressions of 3°C or less. If these calculations are valid, the gradient between the desertic Atacama climate and the much wetter central Chilean climate must have been extremely steep at times in the Quaternary (Paskoff, 1977). Caviedes and Iriarte (1989) have used these projections to develop a verbal model which accounts for the distribution of faunal richness of Cricetid rodents and possibly other mammals in Chile and Argentina. They conclude that the Atacama barrier would have held in the rich, diverse and highly endemic Cricetid faunas (cf. Pierini), forcing whatever dispersal occurred to have been down the eastern (Argentine) side of the mountains in the relatively mesic climates influenced by the tropical flow from the NE. During the periodic episodes when Valdivian vegetation migrated N-ward to the vicinity of 30° in Chile, many of the trans-Andean passes would have been available for faunal migration from E to W. The limited Chilean fauna S of the Atacama can be derived from such movements.

Cricetids resemble butterflies in having greater faunal richness on average E of the Andes, but the resemblances break down on detailed examination. Pierids (except *Eroessa* and *Mathania*) are not forest species and indeed would be excluded from extensively-forested areas. There is no Pierid fauna in archipelagic Chile, and little butterfly fauna at all. The same phenomenon can be seen in the North American Pacific NW rainy belt. For the Cricetid model to account for the Patagonian character of the Chilean Central Valley fauna, the necessary assemblage would have to have been far enough N on the Argen-

tine side to have crossed the passes between 33–30°S (including the Bermejo) when they were sufficiently mesic to be good corridors. There is no concrete evidence bearing on this. See also Heusser, 1983 and Veblen *et al.* 1981.

What we do know of butterflies crossing the Andes is based largely on the passes in the Lake District, which today are mesic and penetrable but were icebound in the Pleistocene. All the movement we can detect has been from W to E in these passes, following climate and prevailing winds. Thus, the hybrid-zone phenomena described for *Tatochila mercedis* and *autodice* are presumably post-Pleistocene in origin. It is striking, however, that populations of *T. m. vanvolxemii* from further N (Copahue and Paso Bermejo-Potrerillos) show signs of previous gene flow from nominate *mercedis* over the crest, though the genitalic morphology that defines such contacts farther S has disappeared. This presupposes the existence of *mercedis* in Chile at least during one fairly recent more mesic interval, and thus implies latitudinal oscillation of ranges. The stranded high-Andean taxa in the Cordón del Viento imply a retreat N-ward with recent drying, as do the ranges of the high-altitude taxa in Salta, Jujuy and Tucumán. (Cei, 1980 discusses some possible biogeographic roles of the *yungas* in the Quaternary.)

"The Argentine provinces of Mendoza and San Juan report 2.5 times as many mammal species as the Chilean provinces at equivalent latitudes" (Caviedes and Iriarte 1989). These provinces are, however, very depauperate insofar as Pierid butterflies are concerned. Although both the timing of S-ward movement and the general routes of dispersal may be similar for Pierids and Cricetids, it is still necessary to account for such striking contradictions in their distributions.

Perspectives on Faunistics. Hayward (1955c) noted that high-Andean elements penetrated the *cuyo* in the Uspallata Valley. Despite the unusually clear overall phytogeographic patterns defined by climate, any attempt to define precise boundaries for the Argentine floras and faunas is bound to be frustrated by the individualistic nature of species distributions. Both the high-Andean and Patagonian floras show abundant evidence of relative youth and evolutionary dynamism, while the Valdivian forest is clearly relictual and ancient. The butterfly faunas treated in this paper have little connection to the Valdivian forest (except *Eroessa chiliensis*), and no butterfly in the region — Pierid or otherwise — is tied by identified sister-group relationships to any other austral region so as to suggest a Gondwanaland-based history. The nearest relative of *Eroessa* is by no means clear. Klots (1932) correctly identifies it as exceedingly primitive in genitalia, venation and form of palpus. Electrophoretically it comes closest to the east-Asian and Indian genus *Hebomoia* Hbn., which shares one probable apomorphic trait with *Hesperocharis* Felder (including *Mathania*); few taxa have been examined in this group of genera (Geiger and Shapiro,

unpublished). There are, however, a variety of suggestive trans-Pacific linkages in Pieridae, which if substantiated would imply considerably greater antiquity for the modern butterflies than has been established in the fossil record; these will be discussed elsewhere.

The traditional geochronology of the Andes has the cold-adapted high-altitude biota, which shows a dominance of circumboreal taxa at the family level (Van der Hammen and Cleef 1987, Raven and Axelrod 1974), entering late in the Pliocene when the latest uplift reached adequate heights to support such a biota. By this view, these organisms have undergone extensive adaptive radiation since the initial phases of the Great American Interchange (Stehli and Webb 1985). It is increasingly clear that this scenario is too simple, and probably largely wrong. More groups have been shown in the fossil record to have arrived in South America from elsewhere before the Interchange, and, more importantly, the amount of differentiation in some high-Andean groups appears too great to be accommodated in so little time. This very large literature is summarized by Briggs (1987), who emphasizes the complexity of patterns observed in different taxonomic groups and their inferred differential antiquity on the continent. The various genera of Andean pierines seem unlikely to have originated and diversified within only 2 or 3 MY — especially since our estimates of the antiquity of *speciation* based on electrophoretic differences tend to fall close to that number (Geiger and Shapiro, unpublished; compare Shapiro and Geiger, 1989 for *Vanessa* across the Isthmus of Panama). But how could cold-adapted genera antedate cold environments? It is of course possible that they arrived on the suggested schedule, but already generically differentiated elsewhere. This requires multiple colonizations by small and weak-flying animals over very great distances. Given the strong morphological affinities to the Asiatic alpine genus *Baltia* Moore, affinities which appear real and not convergent (Field 1958, though the electrophoretic data, such as they are, are ambiguous — Geiger, Michel and Shapiro, unpublished data), some kind of Matthew (1915) "Camelid scenario" appears required. By this view the Asiatic and South American genera were linked across North America and might even have originated there, but subsequently went extinct there. We are unlikely to get fossils to vindicate this scenario, as they have for the Camelidae. But recent evidence (Mercer and Sutter 1982, Clapperton 1983) strongly suggests that Patagonia underwent episodes of glaciation some 7 and 4.6 MYA, before the Ice Ages began in the N Hemisphere (except perhaps in Alaska). This lengthens the potential time-line for the evolution of adaptation to cold in South America, without clarifying the question of where the Pierini came from or who their ancestors might have been.

The genus *Tatochila* is apparently evolving very rapidly right now throughout the Andes, with all sorts of speciation-related phenomena visible, a "ferment of variability" as Dunbar (1968) described the situation in Arctic crustaceans. For a North American butterfly

worker it is strikingly reminiscent of the situation in the *machaon* L. group of *Papilio* — the entities are often not fully speciated, intergrade in complex ways, form hybrid zones, produce local subspecies in some areas and not others, and in general look like sequelae of the Pleistocene (compare Sperling 1987). The data for *Hypsochila* are only beginning to accumulate, but clearly suggest a group in similar if less extensive ferment. The *Phulia* group of taxa are perplexing in that morphospecies tend to appear older than in *Tatochila*, but local populations of the *Phulia nymphula* complex are clearly evolving in a variety of directions, and the various *Infraphulia* and *Pierphulia* look similar. For all these taxa, the genera and subgenera certainly antedate the Pleistocene, speciation may often also, but subspeciation seems to have been working overtime in the Quaternary.[5]

The ultimate interpretation of these radiations will depend on our ability to develop a convincing reconstruction of pierine phylogeny and to determine whence came the stem-species of the various radiations. At present we can say reasonably confidently that *Tatochila*, in its current broad sense, has undergone several radiations, all of which may still be in progress. Certainly the two southernmost (*mercedis* and *theodice*) are, and the next southernmost (*autodice*) is clearly quite active too. The central-Andean/*yungas* taxa are so beset with taxonomic problems that we may infer activity there too, even if we do not understand it. In the far N, *T. xanthodice* Lucas is actively differentiating in different ranges (Ackery 1975). Although we are still not in a position to interpret the extreme rarefaction of the Andean pierines in the N, we can say it is not *de facto* evidence of Gondwanaland origins for the group. Rather, it suggests spread both N and S from a central-Andean center for several genera, though that "center" may not be where they *originated*.

The Fuegian and far-S Patagonian taxa range from the probable ancient relict *Colias ponteni*, to recently-derived and still only weakly-differentiated subspecies in *Tatochila* which as noted above may antedate the inundation of the Straits of Magellan, but perhaps not by much. The mere fact of remoteness in far-southern South America may

[5] The maximum antiquity of *T. m. vanvolxemii* and other taxa of the *monte* can be inferred from recent discussions of the evolution of aridity in Argentina. Volkheimer (1971) inferred humid climates in Patagonia except perhaps semiarid in the modern *pampa* region in the early Tertiary, and again in the Miocene. Axelrod (1979) and Sarmiento (1975) both consider the *monte* and the Patagonian steppe as consequences of the Plio-Pleistocene elevation of the Andes, disagreeing with Solbrig (1976), who feels that arid climates might have existed longer. Since *vanvolxemii* is highly derivative vis-à-vis its relatives, it almost certainly has originated within this time frame. Axelrod (*loc. cit.*) accepts the spotty evidence from Bolivia of an emerging xerophytic-microphyllous vegetation there perhaps as early as the late Eocene, but in any case well-defined by the Miocene. The *Phulias* could thus conceivably go back that far, but whence came their ancestors?

have preserved *Colias ponteni* and *Eroessa chiliensis* — which once may have ranged much more widely, and may indeed have originated elsewhere.

Biogeographers tend to believe what geoscientists tell them about the antiquity of continents and orogenies, a dangerous tendency (though some biogeographers championed continental drift when the geoscientists mainly considered it impossible). In interpreting the distributions and phylogenies of Andean organisms we have always attempted to ram everything into the short time since the late Pliocene, because geoscientists said we had to. Now some glaciologists (Clapperton, Mercer) hold out the possibility of a considerably longer time-line (at least 4, perhaps 6 or 7 million years). Just what this implies for us is still unclear. Nothing in the butterfly data yet *requires* a longer Andean time-line; thanks to the *Baltia* connection we can always make up stories about generic differentiation having occurred elsewhere. And it is clear that much of the evolutionary activity in the Andean-Patagonian Pieridae *is* very young, certainly of Holocene origin. Table 4 summarizes what we might know at the moment, which in terms of data is far greater than what Giacomelli (1915) knew when he published his concluding table, yet not much more definitive!

There is one further approach to these problems, which has not been addressed here. It is strictly ecological and ahistorical and in the "MacArthur tradition," exemplified by the analysis of the Argentine passerine bird fauna by Rabinovich and Rapoport (1975). Neither the size of the Pierid fauna nor the completeness of ground coverage justifies such an analysis at this time. It may ultimately be useful, but it should be obvious that such an approach ignores many of the most interesting and evolutionarily exciting phenomena of faunistics.

Now that we have learned a little more, we can join Giacomelli in lamenting the profundity of our ignorance. Giacomelli wrote even as his compatriots Florentino Ameghino and Francisco P. Moreno were beginning the process of opening up the inescapably complicated geohistorical context in which the Argentine Pierid fauna is imbedded. The ultimate fruits of their labor can be seen in the informed nature of our modern, profound uncertainty.

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	Puna de Atacama (Chile)	Puna de Jujuy/Salta	Cuesta del Obispo/Co.Zapallar	Sierras Pampeanas	Arroyo de Agua Negra	Paso Bermejo	Cordon del Cepo	Precordillera Chilena	Valle Central (Chile)	Precordillera Mendocina	Valles Calchaquies	Cordon del Viento	Chos Malal	Loncopue	Alumine	San Martin - P.N. Lanin	Bariloche - P.N. Nahuel Huapi	Esquel - P.N. Los Alerces	Laguna del Maule	Comodoro Rivadavia - Fitz Roy	Valdivia Region	Rio Gallegos	Rio Grande	Ushuaia - Cordon Martial	Chilean Magallanes
I. ilyodes	X	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
P. r. rosea	X	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
P. r. maria	X	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
P. isabela	X	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
P. nymphula	X	X	X	X	X	X	X	0	0	0	0	X	0	0	0	0	0	0	0	0	0	0	0	0	0
H. penai	X	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
H. w. sulfurodice	X	X	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
H. w. wagenknechti	0	0	0	0	X	X	X	0	0	0	0	0	0	0	0	X	0	0	X	0	0	0	0	0	0
H. galactodice	0	X	0	0	0	0	0	0	0	0	0	X	0	X	X	0	X	X	0	0	0	0	0	0	0
H. huemul	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	X	0	0	X	0	0	0	0	0	0
H. microdice	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	X	X	X	X
H. argyrodice	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	X	0	0	X	X	X
T. t. theodice	0	0	0	0	0	0	0	X	0	0	0	0	0	X	X	X	X	0	X	0	X	0	0	0	0
T. t. gymnodice	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	X	0	X
T. t. staudingeri	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	X	X	X
T. a. autodice	0	0	0	0	0	0	0	0	0	X	X	X	X	X	0	X	X	X	0	X	0	0	0	0	0
T. a. blanchardii	0	0	0	0	0	0	X	X	X	0	0	0	0	0	X	X	X	X	X	0	0	0	0	0	0
T. a. ernestae	X	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
T. m. mercedis	0	0	0	0	0	0	X	X	X	0	0	0	0	0	X	X	0	0	X	0	X	0	0	0	0
T. m. macrodice	X	X	X	X	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
T. m. vanvolxemii	0	0	0	0	0	0	0	0	0	X	X	0	X	X	0	0	0	0	0	X	0	0	0	0	0
T. m. sterodice	0	0	0	0	0	0	0	0	0	0	0	0	0	X	X	X	X	X	0	0	0	X	0	0	X
T. m. fueguensis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	X	X	X	X
T. inversa	0	X	X	X	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
T. orthodice	0	X	X	X	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
T. stigmadice	0	X	X	X	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
T. mariae	X	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
T. d. distincta	0	X	X	X	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
T. d. fieldi	X	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
E. chilensis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	X	X	0	0	0	X	0	0	0	0
M. leucothea	0	0	0	0	0	0	0	X	0	0	0	0	0	0	0	X	X	0	0	0	X	0	0	0	0
C. lesbia	X	X	X	X	0	0	0	0	0	X	X	X	X	X	X	0	X	0	0	X	0	0	0	0	0
C. weberbaueri	X	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
C. blameyi	0	X	X	X	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
C. flaveola	0	0	0	0	X	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
C. vauthieri	0	0	0	0	0	0	X	X	X	0	0	0	X	X	X	X	X	X	X	X	X	X	0	0	X
C. ponteni	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	X
F. deva	X	X	X	X	0	0	0	0	0	0	0	0	0	0	0	0	X	0	0	X	0	0	0	0	0
T. riojana	X	X	X	X	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
# of species:	15	12	10	10	3	2	5	5	3	3	3	4	4	7	7	10	10	5	6	6	5	4	5	4	8

Table 1. Occurrence of selected pierine species in selected areas of Argentina and Chile.
Colias mendozina from the Paso Bermejo is omitted from this and subsequent analyses.

	Puna de Atacama (Chile)	Puna de Jujuy/Salta	Cuesta del Obispo/Co.Zapallar	Sierras Pampeanas	Arroyo de Agua Negra	Paso Bermejo	Cordon del Cepo	Precordillera Chilena	Valle Central (Chile)	Precordillera Mendocina	Valles Calchaquies	Cordon del Viento	Chos Malal	Loncopue	Alumine	San Martin - P.N. Lanin	Bariloche - P.N. Nahuel Huapi	Esquel - P.N. Los Alerces	Laguna del Maule	Comodoro Rivadavia - Fitz Roy	Valdivia Region	Rio Gallegos	Rio Grande	Ushuaia - Cordon Martial	Chilean Magallanes
Puna de Atacama	X	6	5	5	1	1	1	0	0	1	1	2	1	1	1	0	1	0	0	1	0	0	0	0	0
Puna de Jujuy/Salta		X	10	10	1	1	1	0	0	1	1	3	1	2	2	0	2	1	0	1	0	0	0	0	0
Cuesta del Obispo			X	10	1	1	1	0	0	1	1	2	1	1	1	0	1	0	0	1	0	0	0	0	0
Sierras Pampeanas				X	1	1	1	0	0	1	1	2	1	1	1	0	1	0	0	1	0	0	0	0	0
Arroyo de Agua Negra					X	2	2	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Paso Bermejo						X	2	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Cordon del Cepo							X	3	3	0	0	1	1	1	3	4	3	3	2	1	1	1	1	0	1
Precordillera Chilena								X	3	0	0	0	1	2	4	5	4	4	2	1	3	1	0	0	1
Valle Central (Chile)									X	0	0	0	3	1	3	3	2	2	3	1	2	1	0	0	1
Precordillera Mendocina										X	3	2	3	3	1	1	2	1	0	3	0	0	0	0	0
Valles Calchaquies											X	2	3	3	1	1	2	2	0	3	0	0	0	0	0
Cordon del Viento												X	2	3	3	1	3	2	0	2	0	0	0	0	0
Chos Malal													X	4	2	2	2	3	1	4	2	1	0	0	1
Loncopue														X	5	4	4	4	2	4	2	2	1	0	2
Alumine															X	5	6	4	4	2	3	2	1	0	2
San Martin de los Andes - Parque Nacional Lanin																X	7	4	5	2	5	2	1	0	2
San Carlos de Bariloche - Parque Nacional Nahuel Huapi																	X	5	3	4	4	2	0	0	2
Esquel - Parque Nacional Los Alerces																		X	2	2	1	2	0	0	2
Laguna del Maule																			X	1	3	1	0	0	1
Comodoro Rivadavia - Fitz Roy																				X	1	0	1	0	2
Valdivia Region																					X	1	0	0	4
Rio Gallegos																						X	2	2	4
Rio Grande																							X	2	2
Ushuaia - Cordon Martial																								X	4
Chilean Magallanes																									X

Table 2. Numbers of species shared by all possible pairs of regions. Data from table 1.

	Puna de Atacama (Chile)	Puna de Jujuy/Salta	Cuesta del Obispo/Co.Zapallar	Sierras Pampeanas	Arroyo de Agua Negra	Paso Bermejo	Cordón del Cepo	Precordillera Chilena	Valle Central (Chile)	Precordillera Mendocina	Valles Calchaquíes	Cordón del Viento	Chos Malal	Loncopué	Aluminé	San Martín - P.N. Lanín	Bariloche - P.N. Nahuel Huapí	Esquel - P.N. Los Alerces	Laguna del Maule	Comodoro Rivadavia - Fitz Roy	Valdivia Region	Río Gallegos	Río Grande	Ushuaia - Cordón Martial	Chilean Magallanes
Puna de Atacama (Chile)	+	.286	.250	.250	.059	.063	.053	.000	.000	.059	.059	.118	.056	.048	.048	.000	.042	.000	.000	.050	.000	.000	.000	.000	.000
Puna de Jujuy/Salta		+	.833	.833	.071	.077	.063	.000	.000	.071	.071	.230	.067	.118	.118	.000	.100	.063	.000	.059	.000	.000	.000	.000	.000
Cuesta del Obispo/Co.Zapallar			+	1.000	.083	.091	.071	.000	.000	.083	.083	.167	.077	.063	.063	.000	.053	.000	.000	.067	.000	.000	.000	.000	.000
Sierras Pampeanas				+	.083	.091	.071	.000	.000	.083	.083	.167	.077	.063	.063	.000	.053	.000	.000	.067	.000	.000	.000	.000	.000
Arroyo de Agua Negra					+	.500	.333	.000	.000	.000	.000	.167	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
Paso Bermejo						+	.667	.000	.250	.000	.000	.200	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
Cordón del Cepo							+	.429	.600	.000	.000	.125	.125	.091	.333	.364	.250	.430	.222	.100	.111	.125	.111	.000	.083
Precordillera Chilena								+	.600	.000	.000	.000	.125	.200	.500	.500	.364	.667	.222	.100	.430	.125	.000	.000	.083
Valle Central (Chile)									+	.000	.000	.000	.750	.111	.429	.300	.182	.286	.500	.125	.333	.167	.000	.000	.100
Precordillera Mendocina										+	1.000	.400	.750	.429	.111	.083	.182	.333	.000	.500	.000	.000	.000	.000	.000
Valles Calchaquíes											+	.400	.750	.429	.111	.083	.182	.333	.000	.500	.000	.000	.000	.000	.000
Cordón del Viento												+	.333	.375	.375	.077	.273	.286	.000	.250	.000	.000	.000	.000	.000
Chos Malal													+	.571	.222	.167	.167	.500	.111	.667	.286	.143	.000	.000	.091
Loncopué														+	.556	.308	.308	.500	.182	.444	.200	.200	.091	.000	.154
Aluminé															+	.417	.545	.500	.444	.182	.333	.222	.091	.000	.154
San Martín - P.N. Lanín																+	.539	.364	.455	.143	.500	.167	.072	.000	.125
Bariloche - P.N. Nahuel Huapí																	+	.500	.231	.333	.364	.167	.000	.000	.125
Esquel - P.N. Los Alerces																		+	.222	.222	.111	.286	.000	.000	.182
Laguna del Maule																			+	.091	.375	.111	.000	.000	.077
Comodoro Rivadavia - Fitz Roy																				+	.100	.000	.100	.000	.167
Valdivia Region																					+	.125	.000	.000	.444
Río Gallegos																						+	.286	.333	.500
Río Grande																							+	.286	.182
Ushuaia - Cordón Martial																								+	.500
Chilean Magallanes																									+

Table 3. Sørensen's index of similarity used to compare all possible pairs of faunas from Table 2. These data are presented as a dendrogram in Fig. 23.

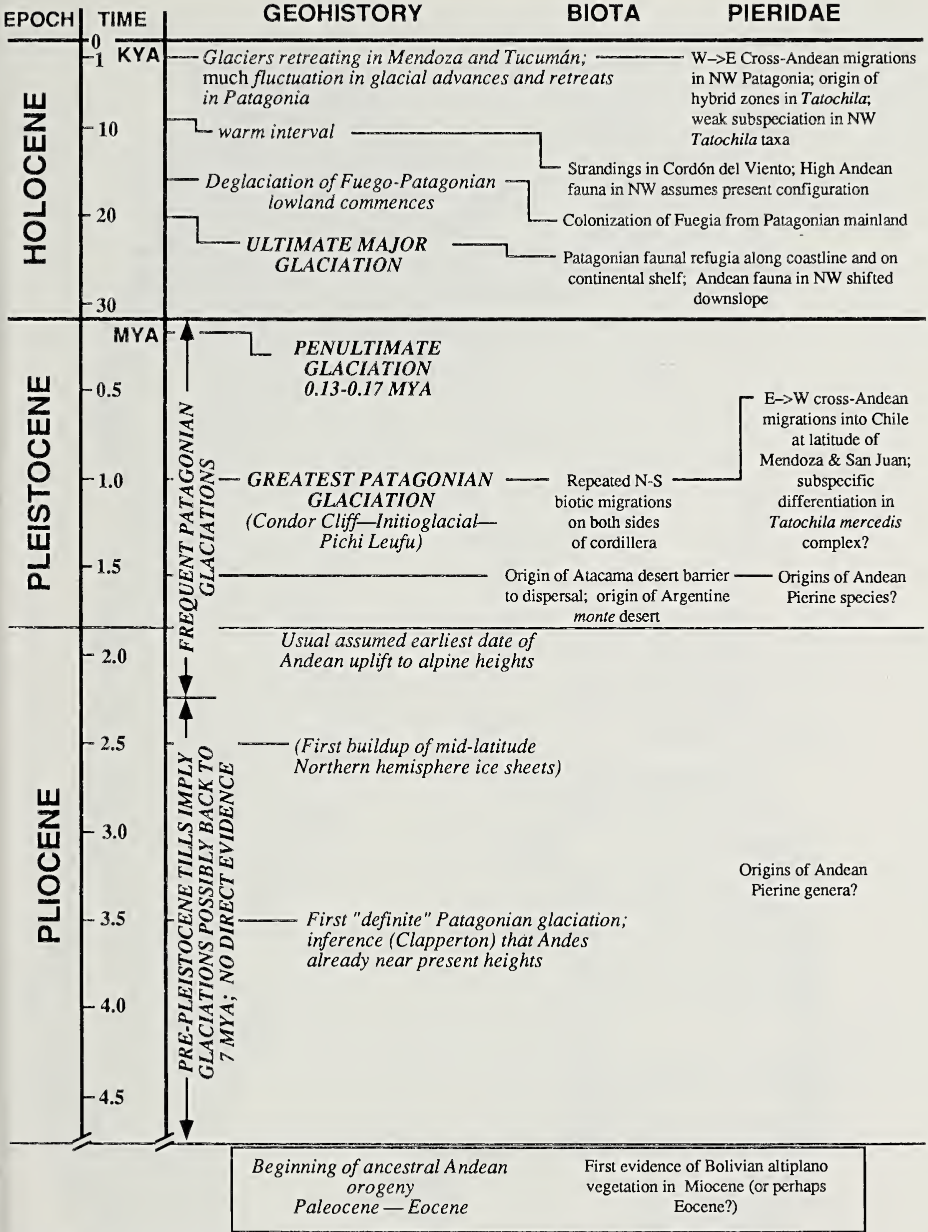


Table 4. Attempted cross-correlation of geohistorical and biotic events in the southern Andes and Patagonia with development of the Pierid butterfly fauna. KYA = thousands of years ago; MYA = millions of years ago. Note discrepancy between the usual Plio-Pleistocene estimate for the origin of alpine habitats in the Andes and the much older estimate inferred by Mercer and Clapperton from alleged pre-Pleistocene tills, and the older-still earliest paleobotanical evidence for xerophytic vegetation in Bolivia. Very detailed paleoclimatic sequences are available for the Holocene in much of southern South America, but the quality and quantity of evidence diminish with time. Pre-Pleistocene events are in part inferred by cross-correlation with evidence bearing on marine temperatures near New Zealand (see Clapperton reference).

Fig. 1. Political map of Argentina.

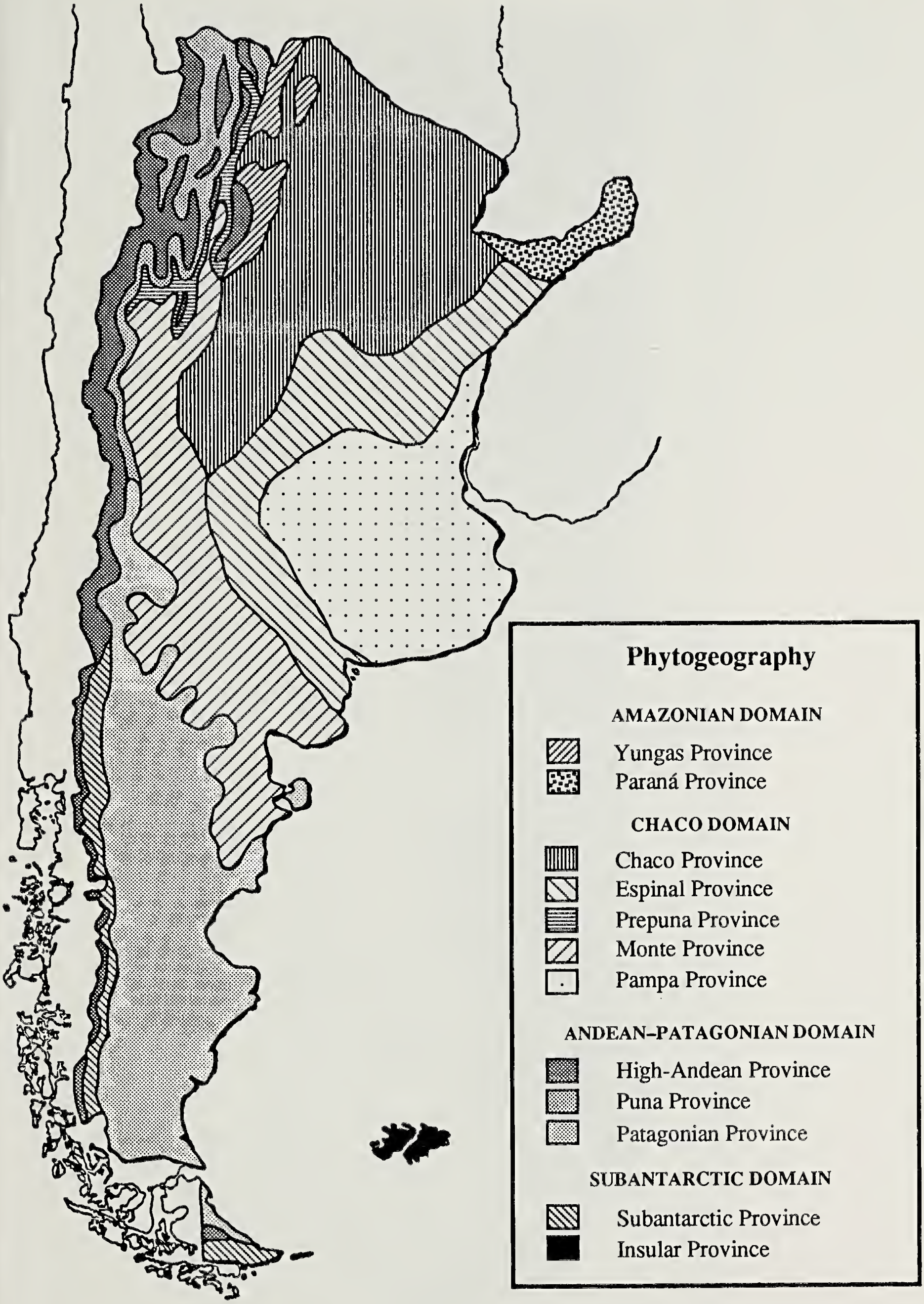


Fig. 2. Phytogeography of Argentina, redrawn from Cabrera, 1971. Fig. 1.

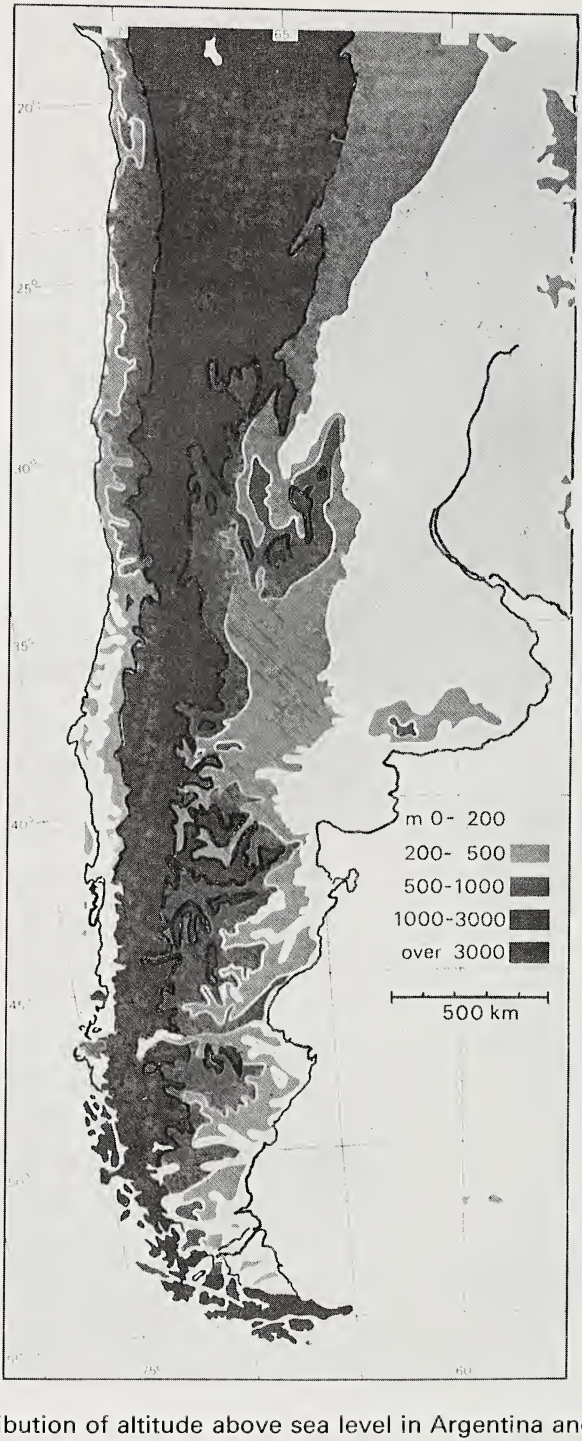


Fig. 3. Distribution of altitude above sea level in Argentina and Chile, from Madsen *et al.*, 1980.

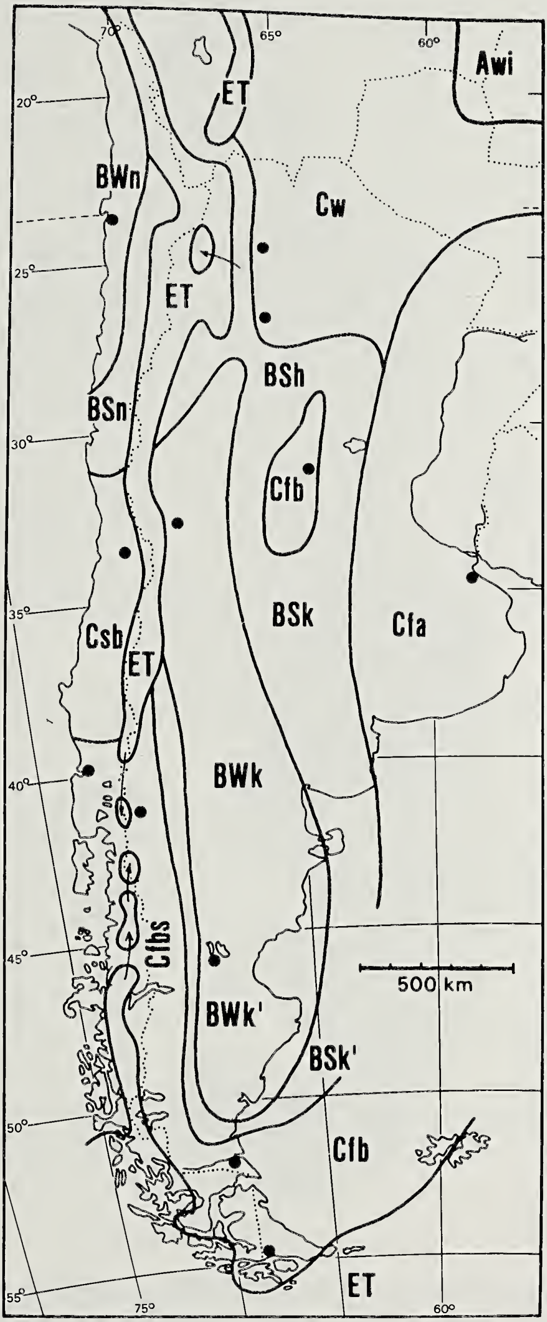


Fig. 4. Climate types of Argentina and Chile according to the Köppen system, from Madsen *et al.*, 1980.

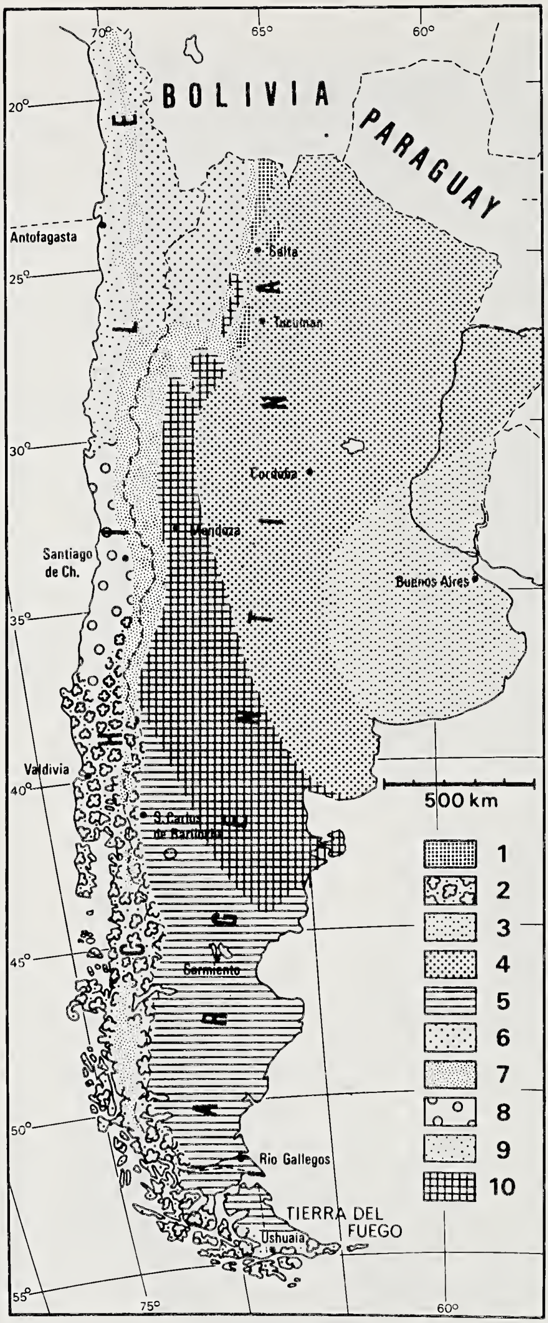


Fig. 5. Phytogeography of Argentina and Chile as mapped by Madsen *et al.*, 1980. Key: 1. Subtropical forest; 2. Subantarctic (mostly *Nothofagus*) forest; 3. Pampa; 4. Xerophytic woodland and scrub (Espinal); 5. Patagonian steppe; 6. Puna; 7. Andean boreal and nival zones; 8. Chilean Mediterranean scrub (Matorral) and valley grassland; 9. Atacama Desert; 10. Monte Desert and arid montane (Prepuna). Compare Fig. 2.

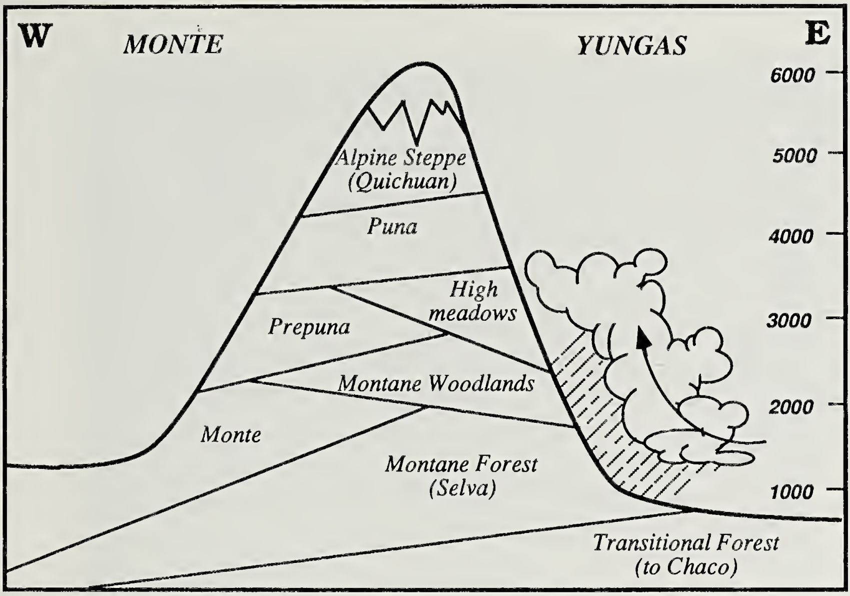


Fig. 6. Generalized distribution of vegetation types in NW Argentina, reflecting orographic influences on precipitation. Redrawn from Cabrera, 1971.

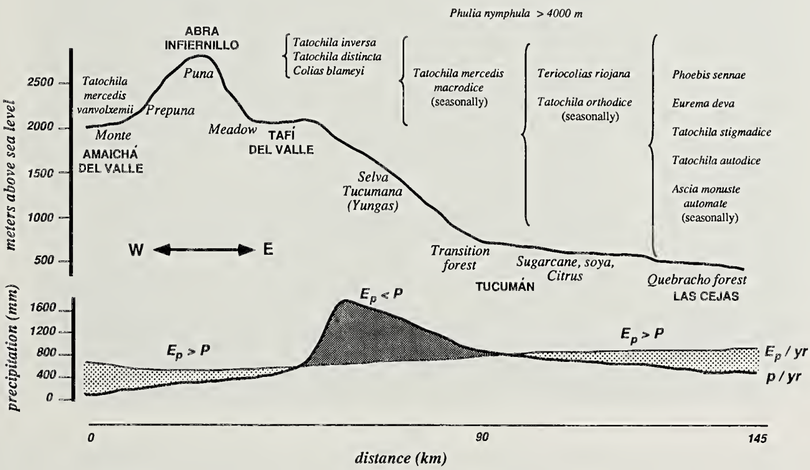


Fig. 7. Transect across the *Sierras Pampeanas* in Tucumán, showing vegetation types, altitudinal distribution of Pieridae, and relationship of Precipitation (P) to Potential Evapotranspiration (E_p) (annualized). *Phulia nymphula* occurs only on the peaks over 4000 m, not reaching the level of Abra Infiernillo. Partially redrawn after Madsen *et al.* (1980).

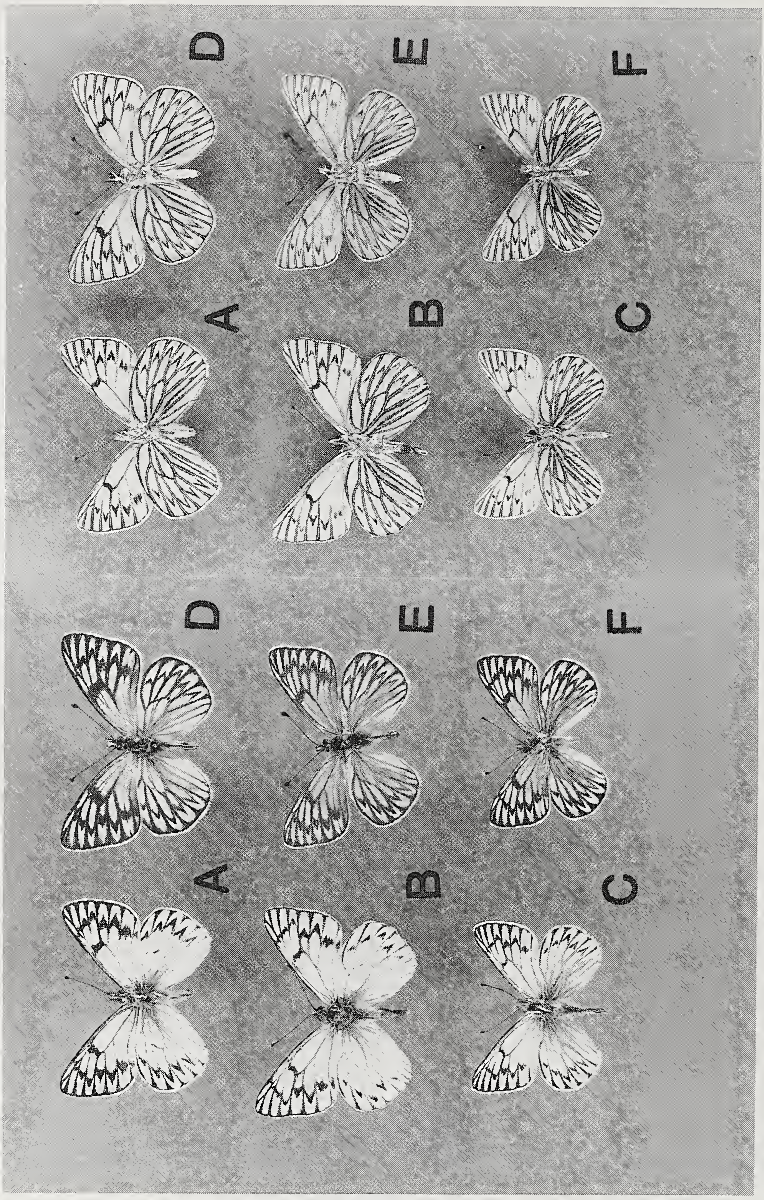


Fig. 8. *Tatochila theodice* along a latitudinal cline. A–C, males; D–F, females. A, Loncopué, Neuquén, 8.XI.1988 (first brood) (N-most known population of nominate *theodice* in Argentina). B, La Esperanza, Santa Cruz, 15.I.1979 (DE) (2nd brood) (± *gymnodice*). C, Río Grande, Tierra del Fuego, 25.XI.1988 (1st brood) (± *staudingeri*). D, Puerto Blest, Parque Nacional Nahuel Huapí, Río Negro, 28.II.1979 (DE) (2nd brood?) (*theodice*). E, Lago Argentino, Santa Cruz, 11.I.1979 (DE) (2nd brood?) (± *gymnodice*). F, Río Grande, Tierra del Fuego, 25.XI.1988 (1st brood) (± *staudingeri*).

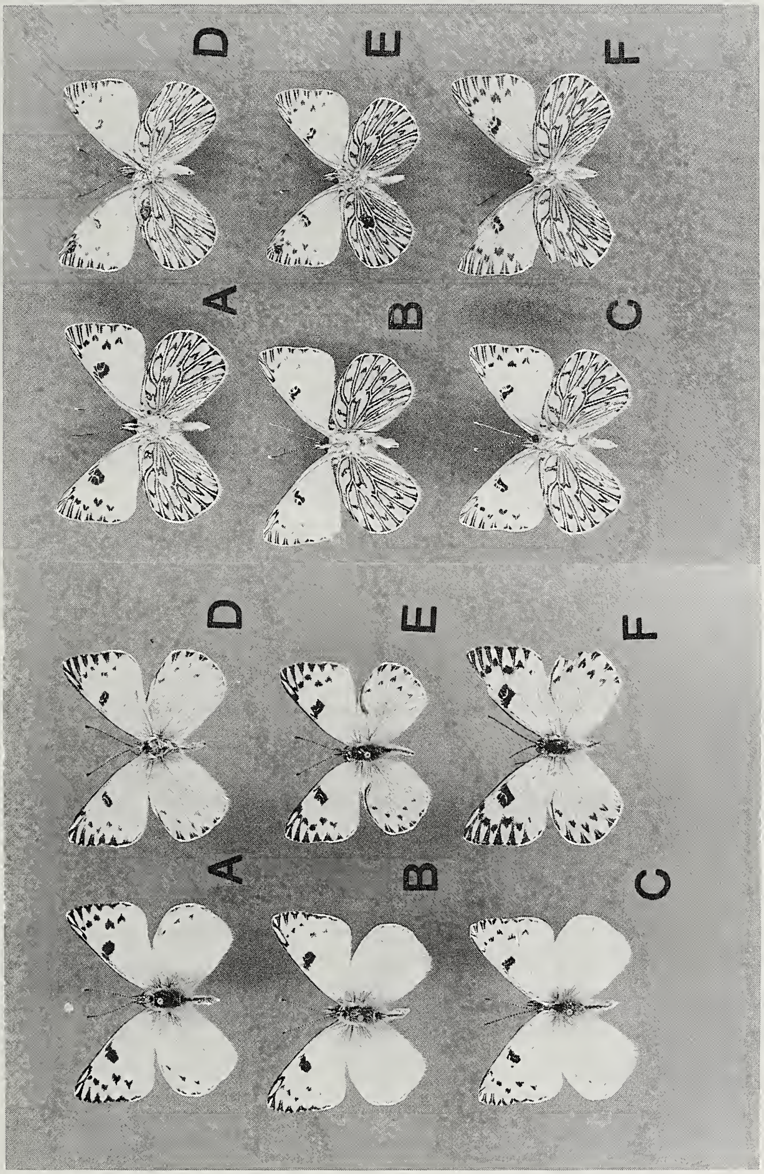
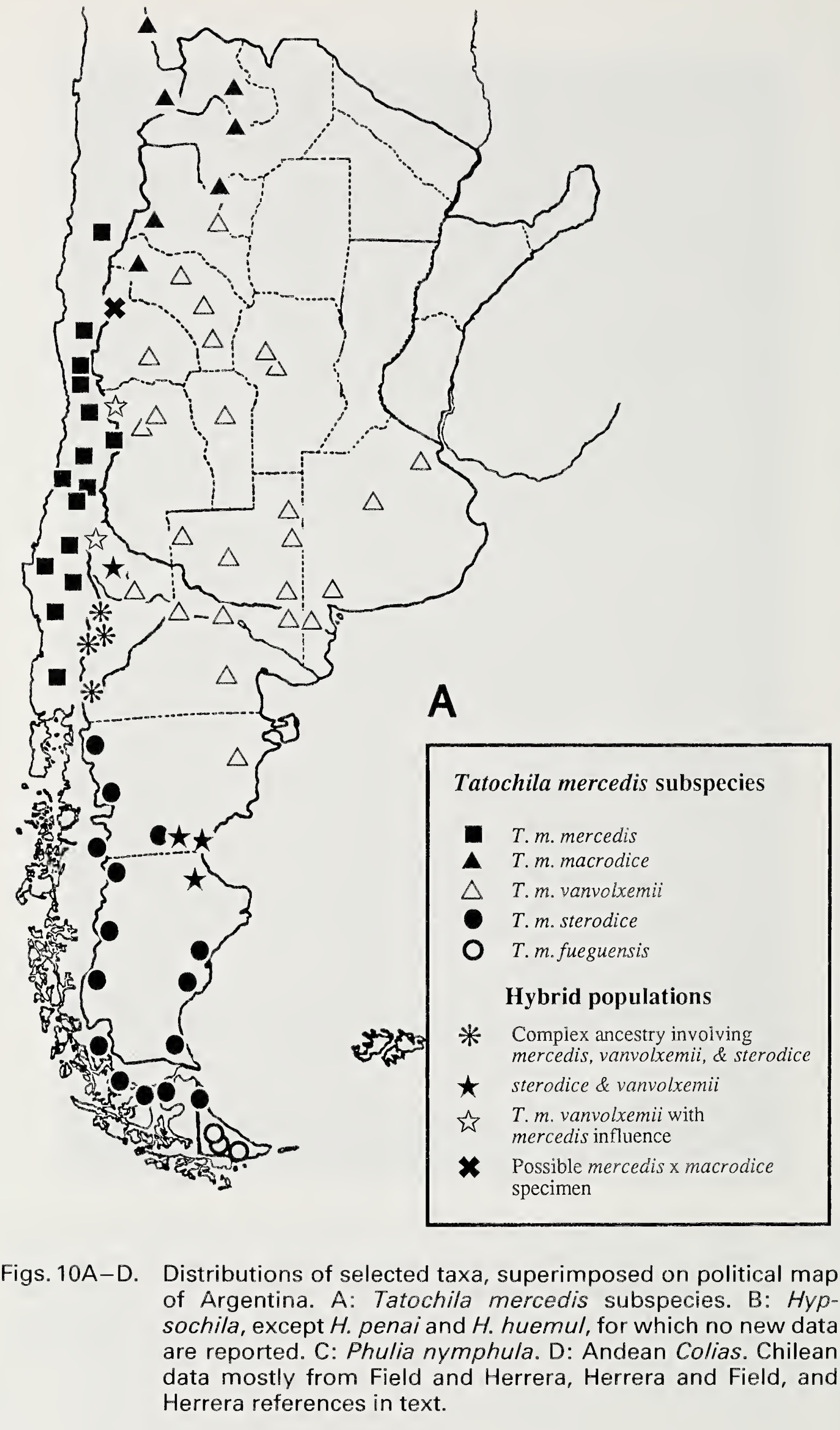
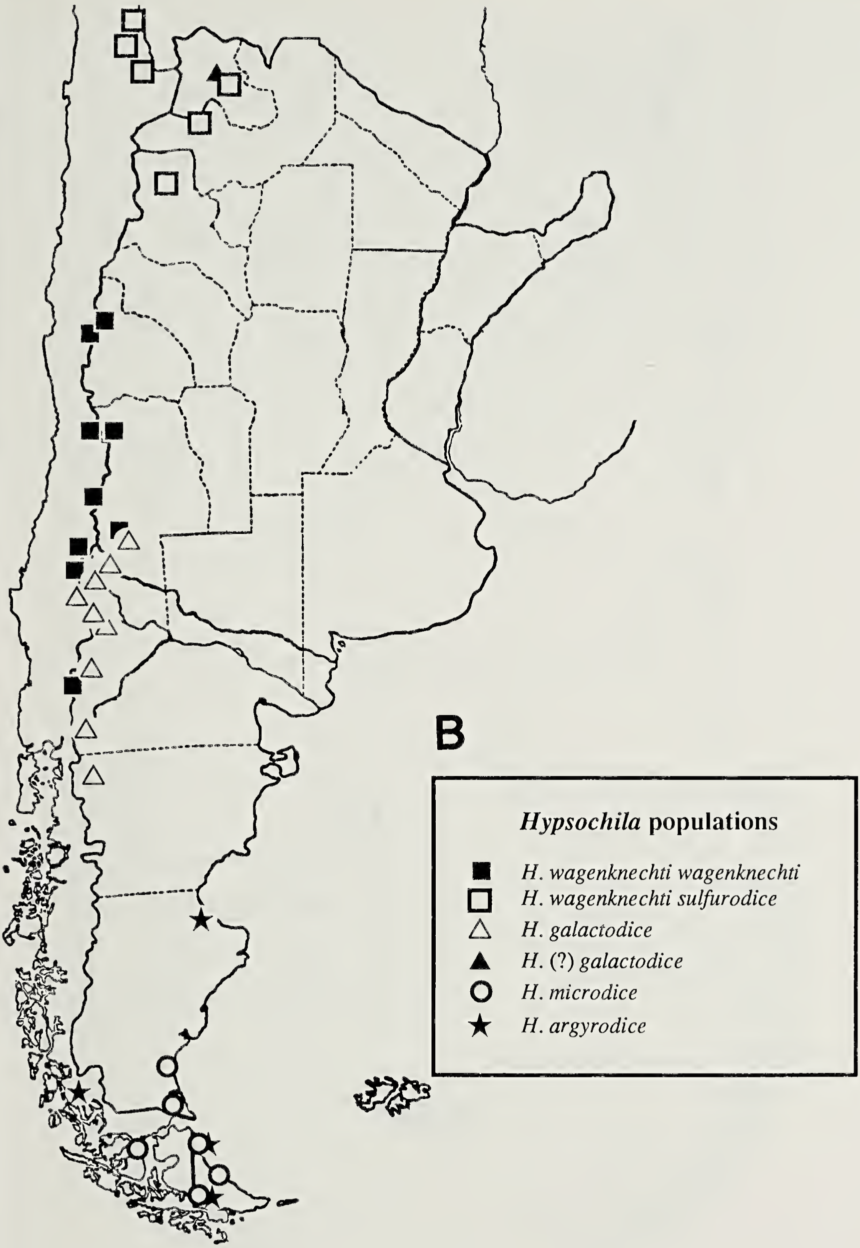
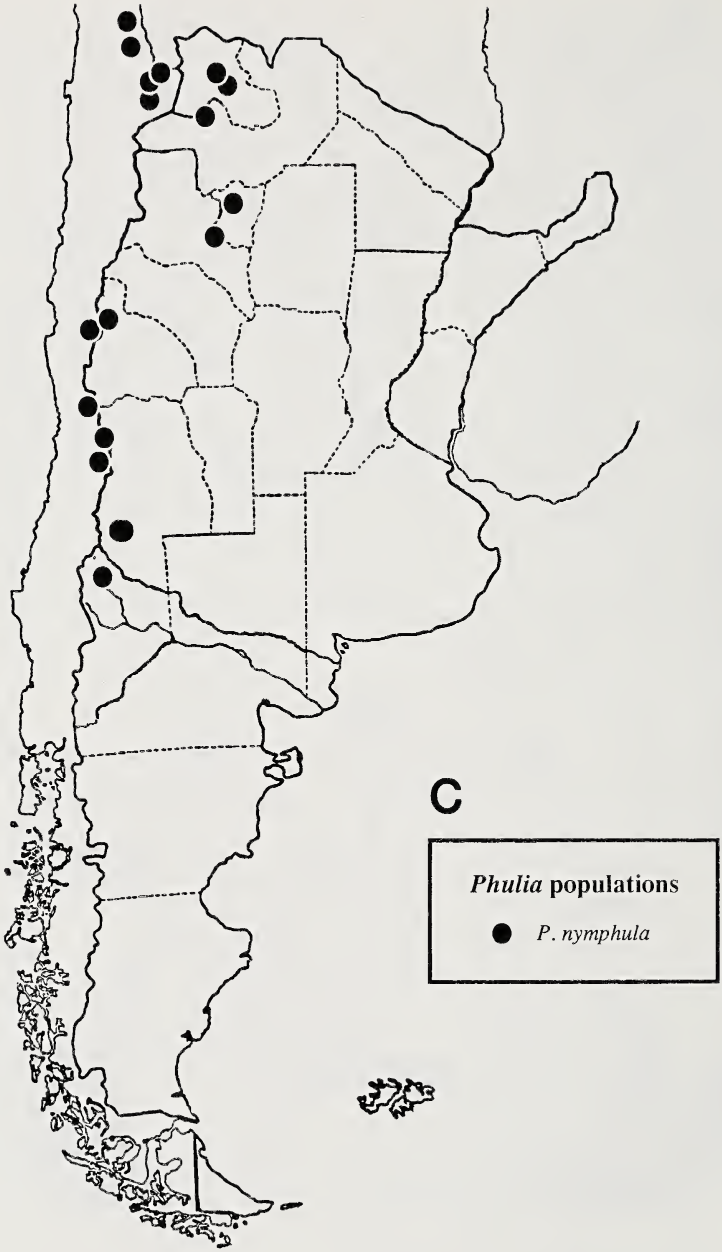


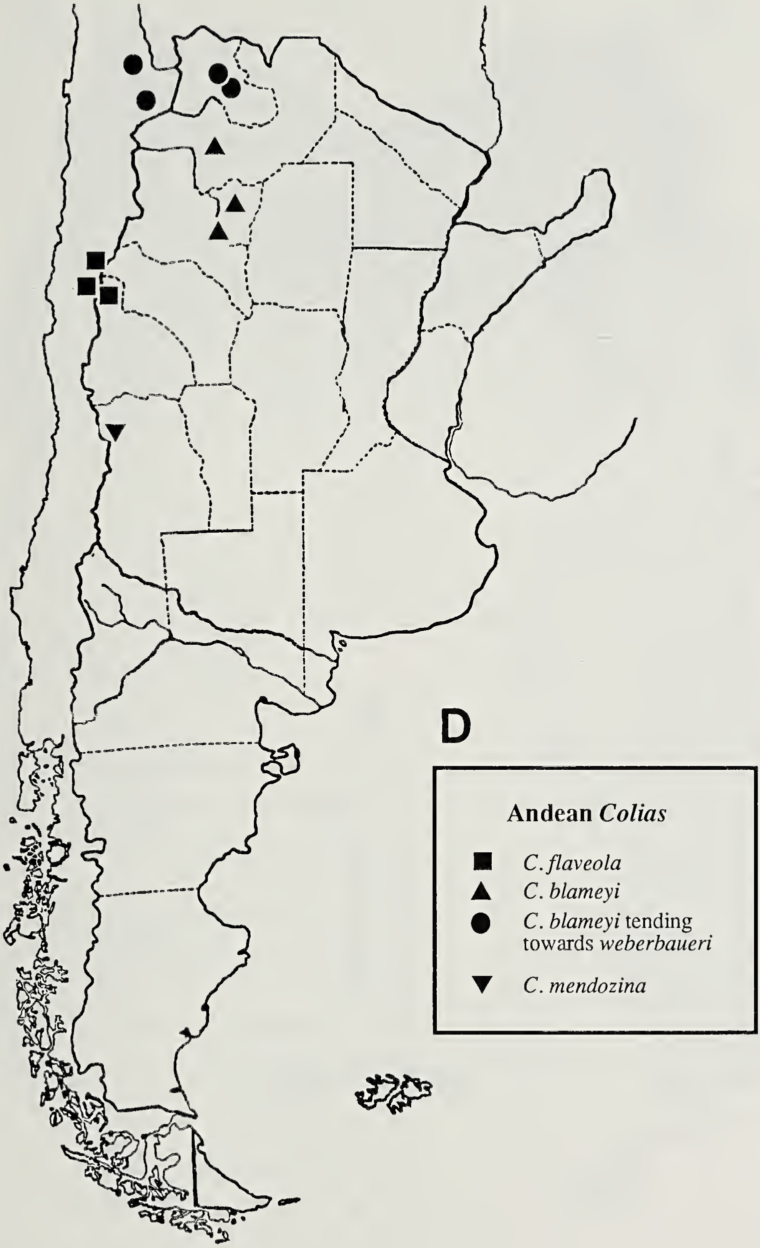
Fig. 9. *Tatochila autodice — blanchardii* intergrades reared from wild ova collected in the NW Patagonian hybrid zone, XI.1988. A–C, males; D–F, females. A, D, E from Esquel, Chubut; B, C, F from San Carlos de Bariloche, Río Negro. Specimens A and F are within the range of variation of pure Chilean *blanchardii*. See Shapiro, 1986a for characters.



Figs. 10A–D. Distributions of selected taxa, superimposed on political map of Argentina. A: *Tatochila mercedis* subspecies. B: *Hypsochila*, except *H. penai* and *H. huemul*, for which no new data are reported. C: *Phulia nymphula*. D: Andean *Colias*. Chilean data mostly from Field and Herrera, Herrera and Field, and Herrera references in text.


B
Hypsochila populations
H. wagenknechti wagenknechti
H. wagenknechti sulfurodice
H. galactodice
H. (?) galactodice
H. microdice
H. argyrodice


C
Phulia populations
P. nymphula


D
Andean *Colias*
C. flaveola
C. blameyi
C. blameyi tending towards *weberbaueri*
C. mendozina

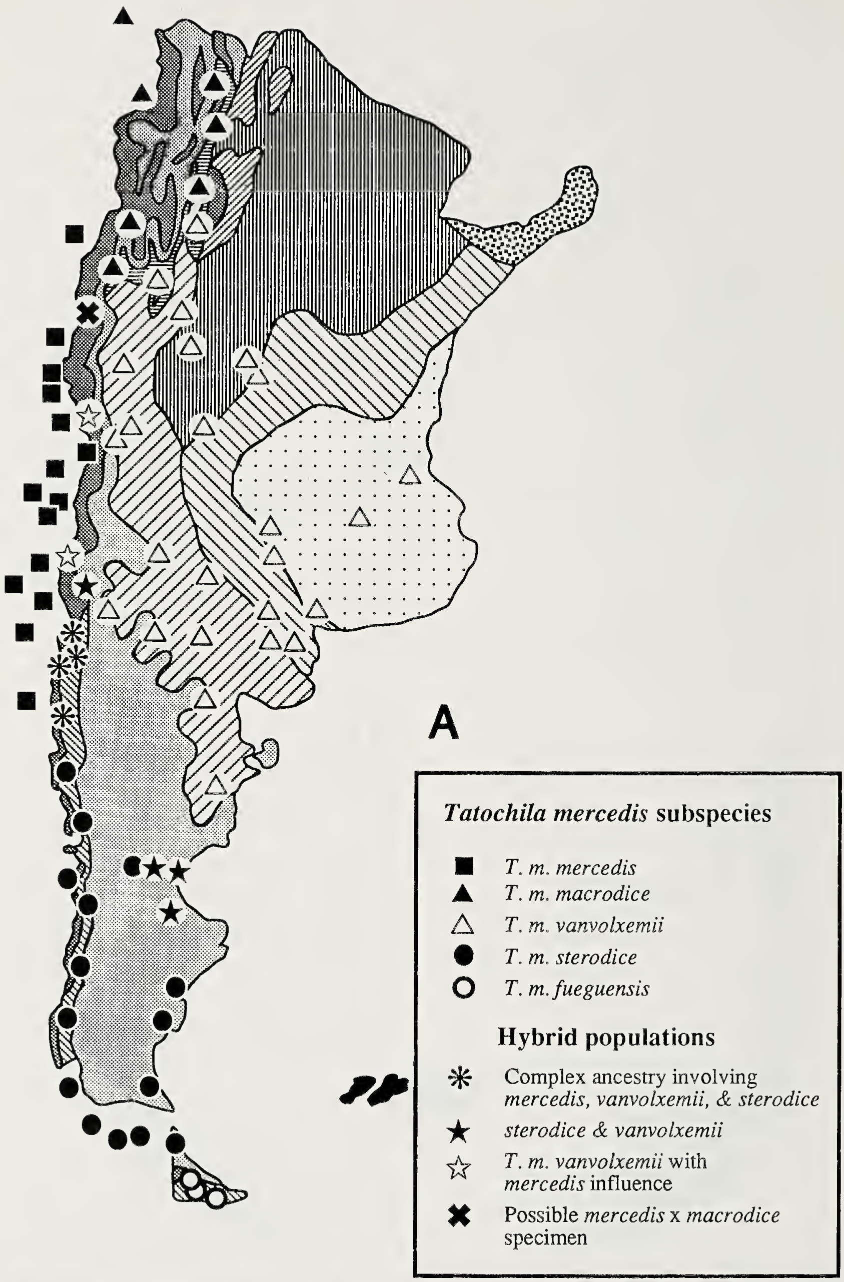
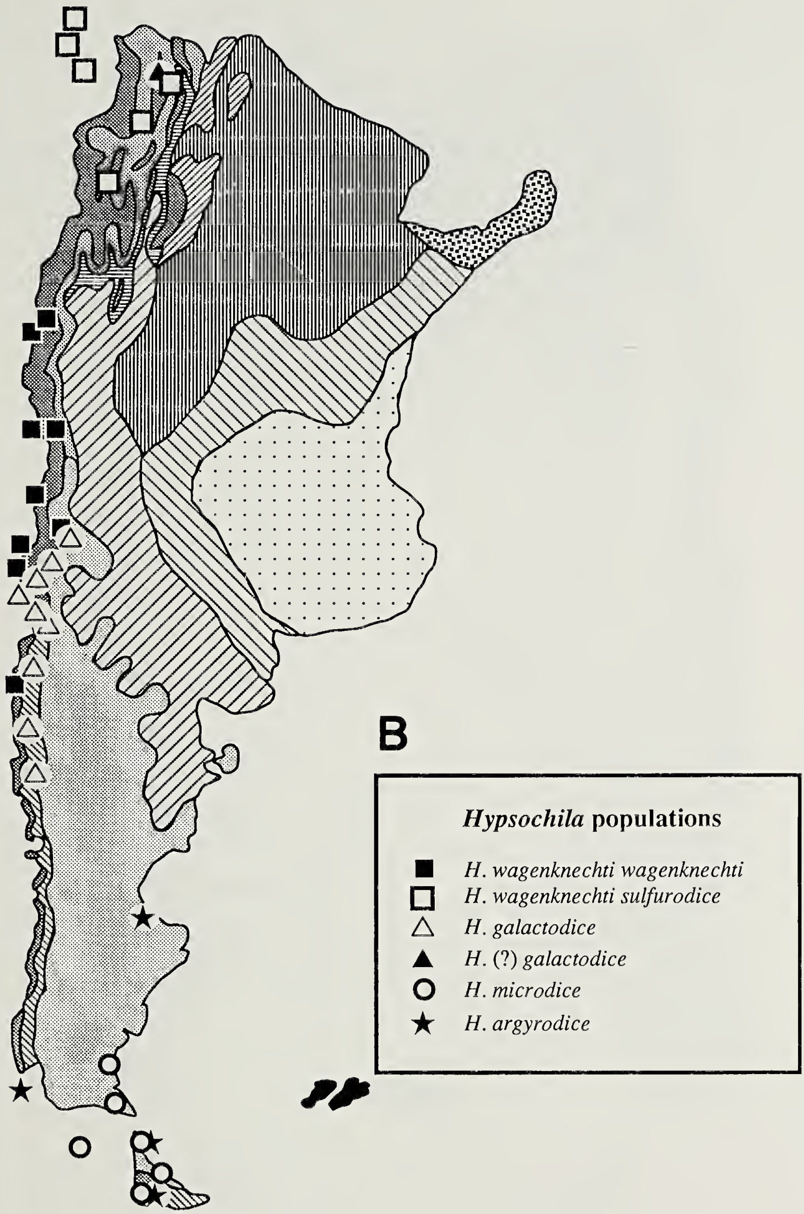
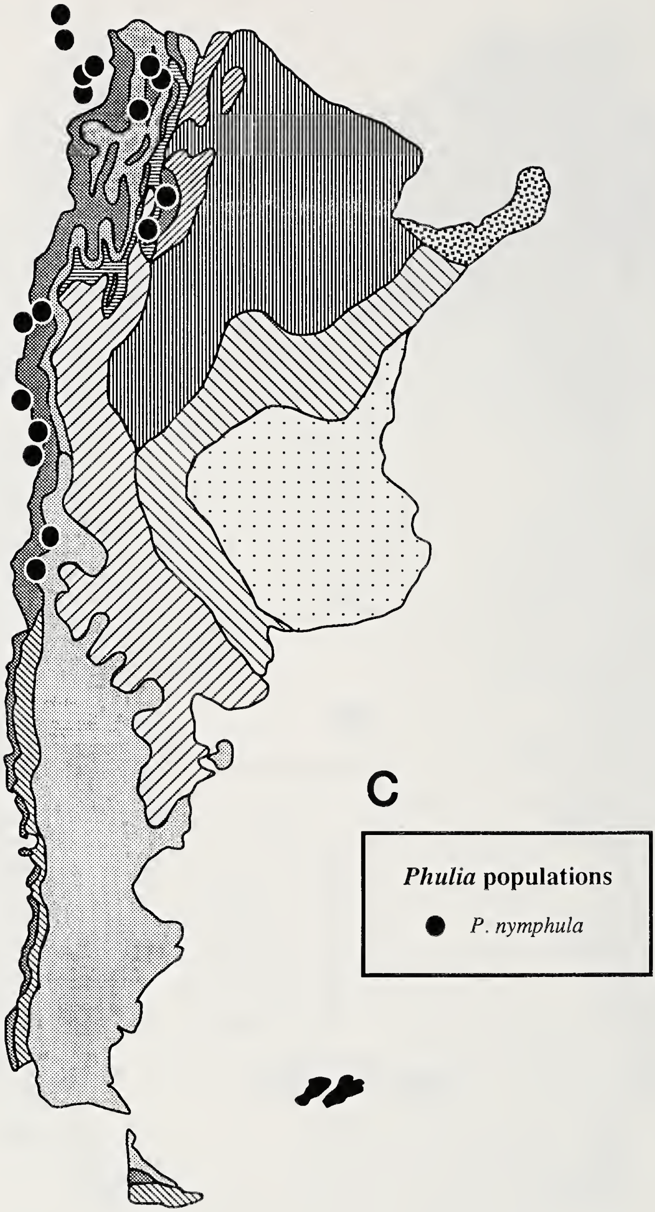


Fig. 11A–D. Distributions of selected taxa, superimposed on phytogeography as mapped by Cabrera, 1971 (cf. Fig. 2). A: *Tatochila mercedis* subspecies. B: *Hypsochila*, except *H. penai* and *H. huemul*. C: *Phulia nymphula*. D: Andean *Colias*. Note the absence of *Hypsochila* from the *Sierras Pampeanas*.


B
Hypsochila populations
H. wagenknechti wagenknechti
H. wagenknechti sulfurodice
H. galactodice
H. (?) galactodice
H. microdice
H. argyrodice


C
Phulia populations
P. nymphula

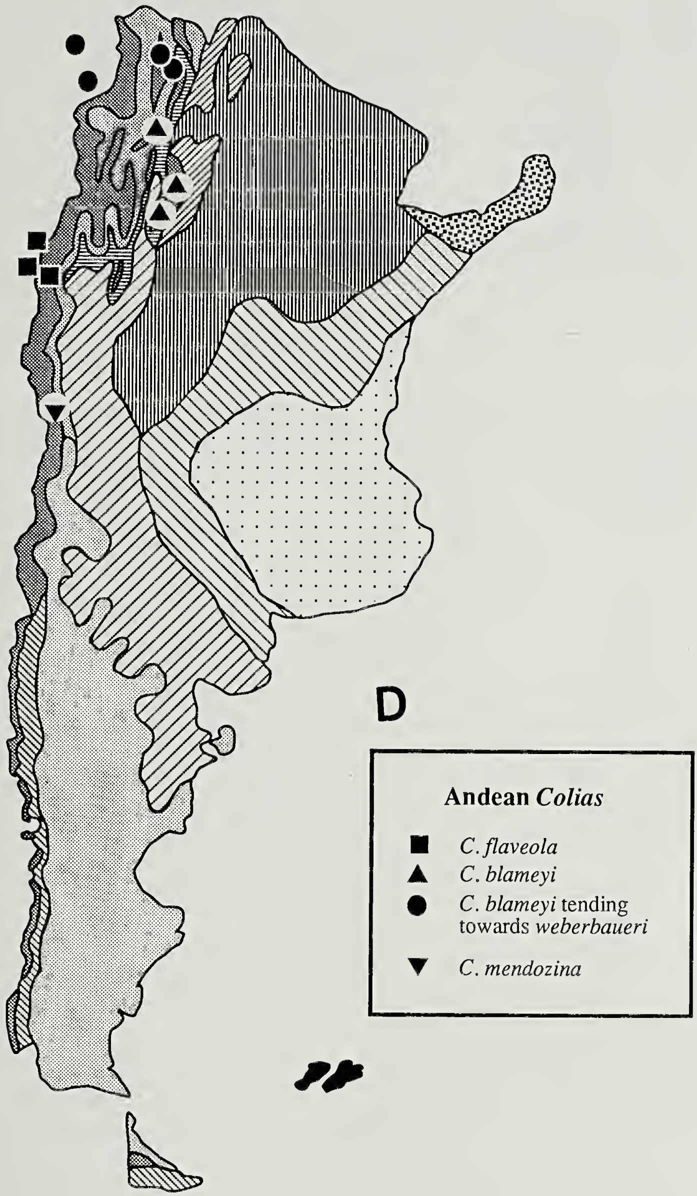

D
Andean Colias
C. flaveola
C. blameyi
C. blameyi tending towards weberbaueri
C. mendozina

Fig. 12. Unusual male (*mercedis* — *macrodice* intergrade?) not fitting any named entity in polytypic species *Tatochila mercedis*. Arroyo de Agua Negra, San Juan, 3.XI.1988.

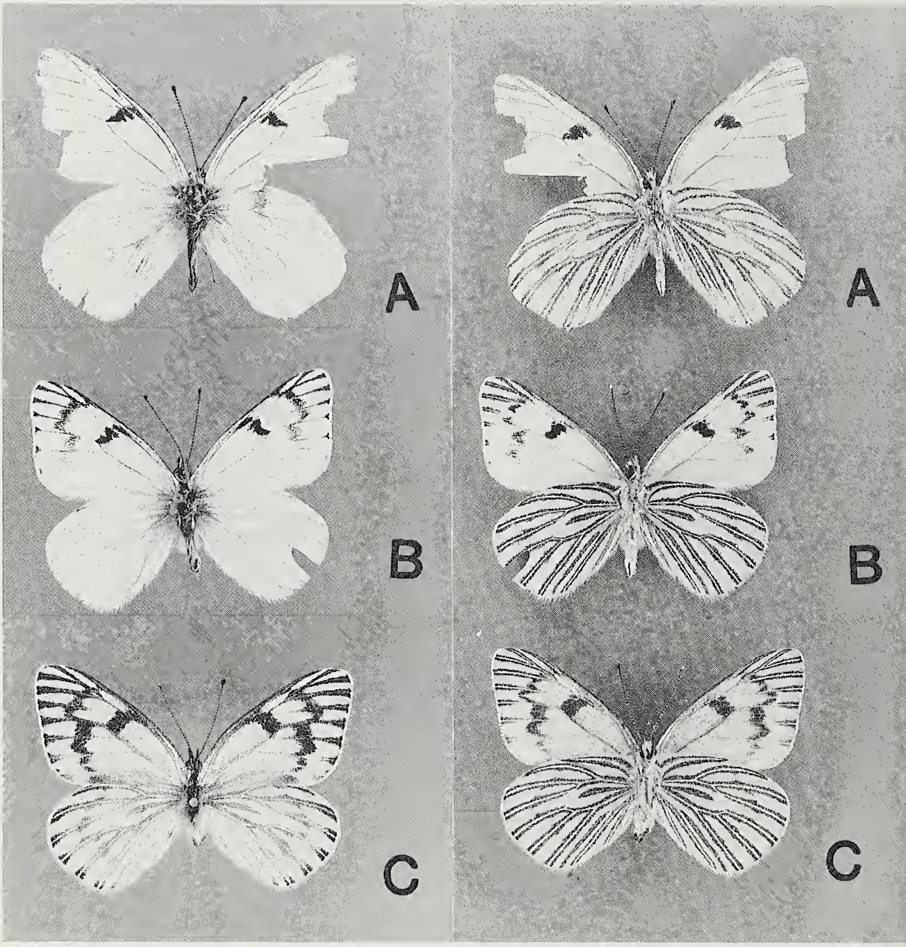


Fig. 13. Wild-collected first-brood males (A, B) and female (C) of *Tatochila mercedis vanvolxemii* from Zapala, Neuquén, 7.XI.1988. Note variable loss of apical FW markings and tendency of these to form a continuous line if present.

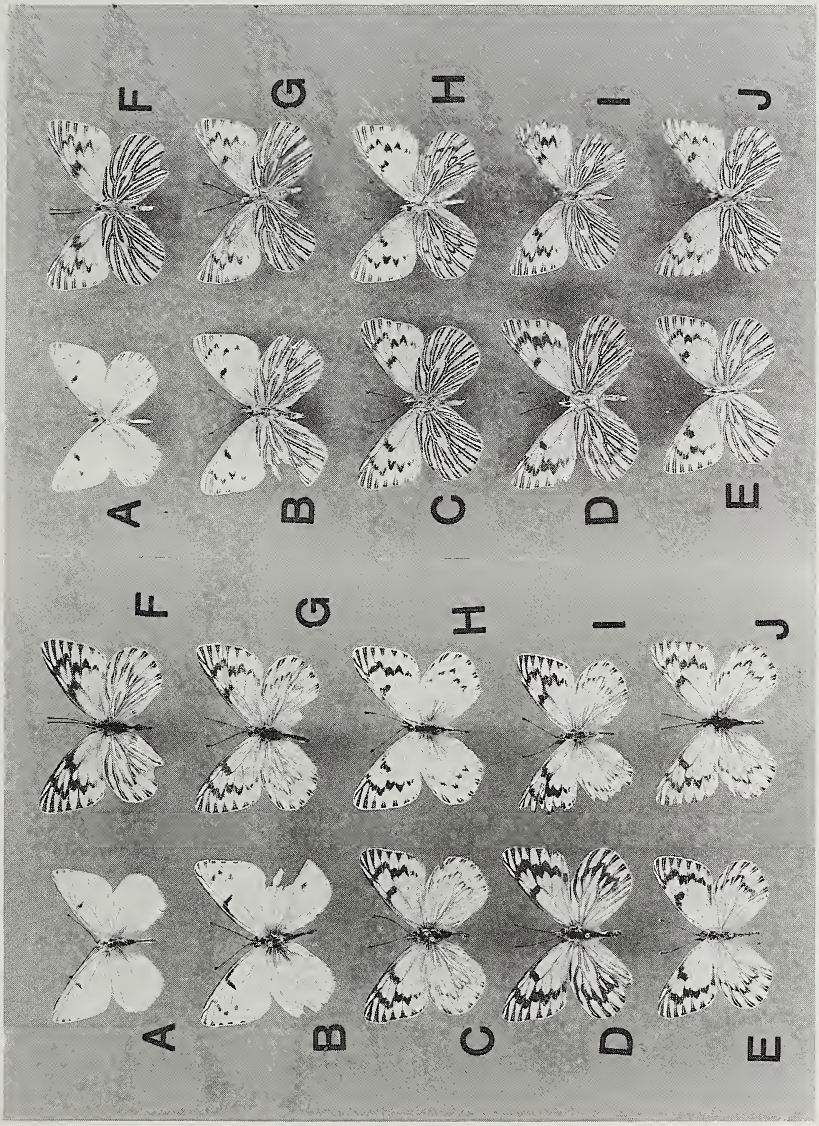


Fig. 14. *Tatochila mercedis vanvolxemii* — *sterodice* intergrades from Loncopué, Neuquén, 8.XI.1988, all collected in the same field. A, B males; remainder females; first brood.

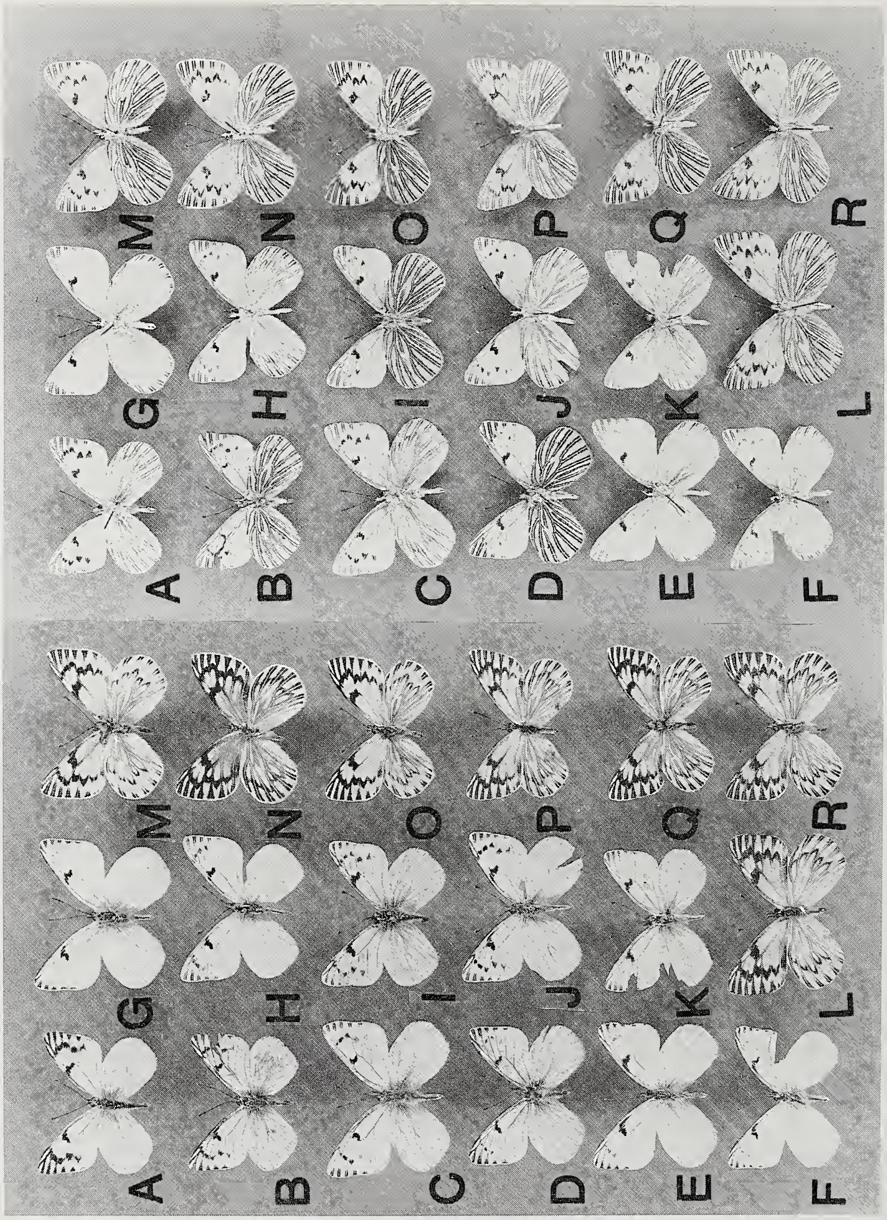


Fig. 15. *Tatochila mercedis vanvolxemii* — *sterodice* intergrades from Barrio Próspero Palazzo, Comodoro Rivadavia, Chubut, 19.XI.1988, all collected in close proximity. A–K, males; L–R, females. Most of these phenotypes are outside the range of variation of "pure" *vanvolxemii*; note tendency of apical FW markings in males to form discrete dots. First brood.

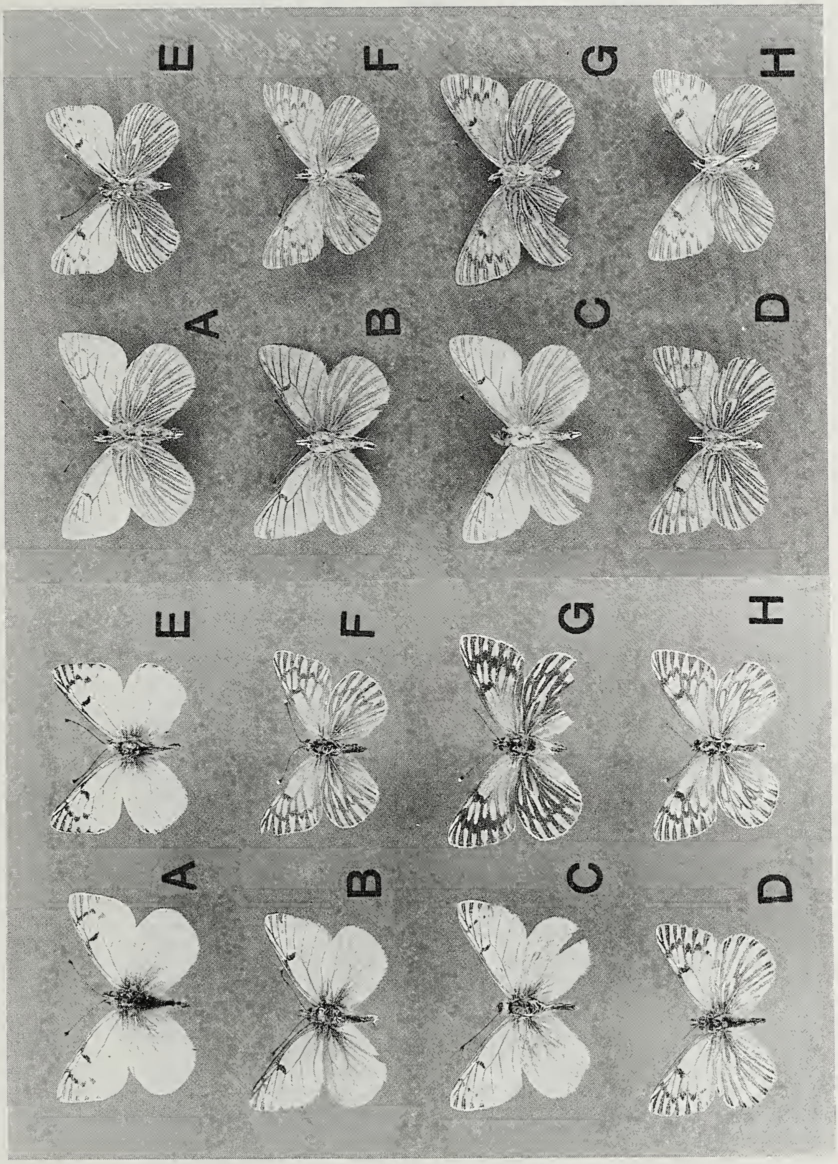


Fig. 16. Intergradation of *Tatochila mercedis sterodice* and *T. m. fueguensis*. A, B, C, E, males; D, F, G, H females. A, Lago Fagnano, Tierra del Fuego, 19.I.1979 (DE) (intermediate). E, Cte. Luis Piedrabuena, Santa Cruz, 20.XI.1988 (*sterodice*). All others from La Esperanza, Santa Cruz, 130 km NW Río Gallegos, 15.I.1979 (DE) (complete intergradation).

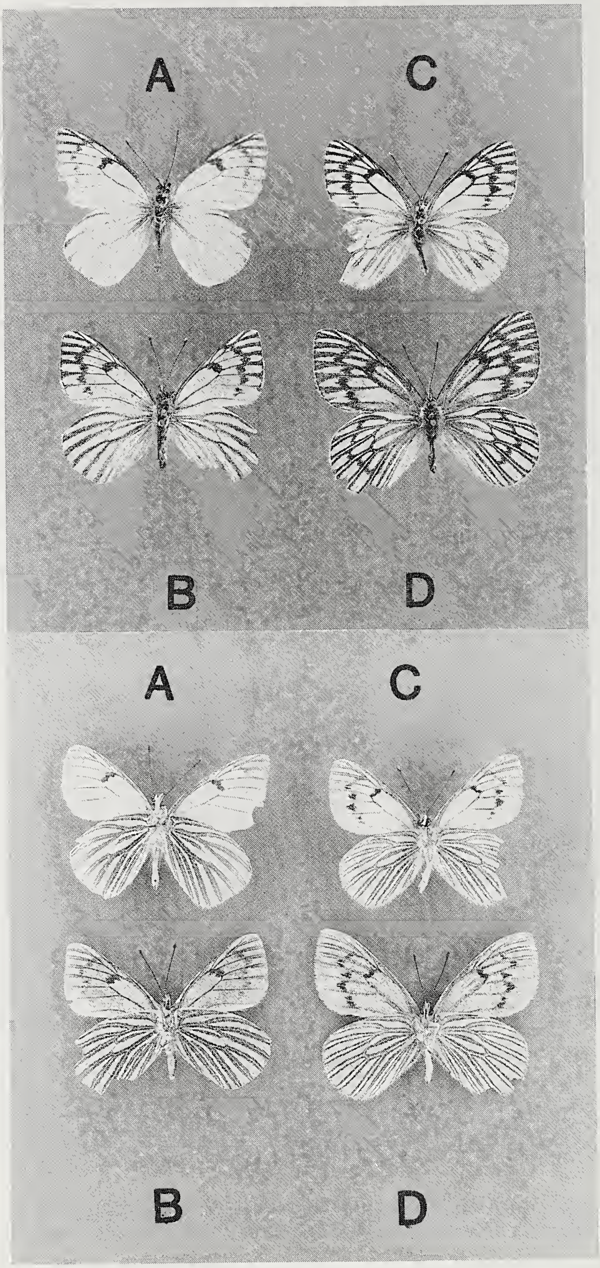


Fig. 17. High-altitude *Tatochila* from NW Argentina. A, *T. inversa* male, Cerro Amarillo, Jujuy, 4.I.1980 (RE). B, *T. inversa* female, Cerro Zapallar, Salta, 22.I.1986. C, *T. distincta distincta* male, Abra Infiernillo, Tucumán, 20.I.1986. D, *T. distincta*, female, Cerro Zapallar, Salta, 22.I.1986. The male *inversa* is the first figured from Argentina.

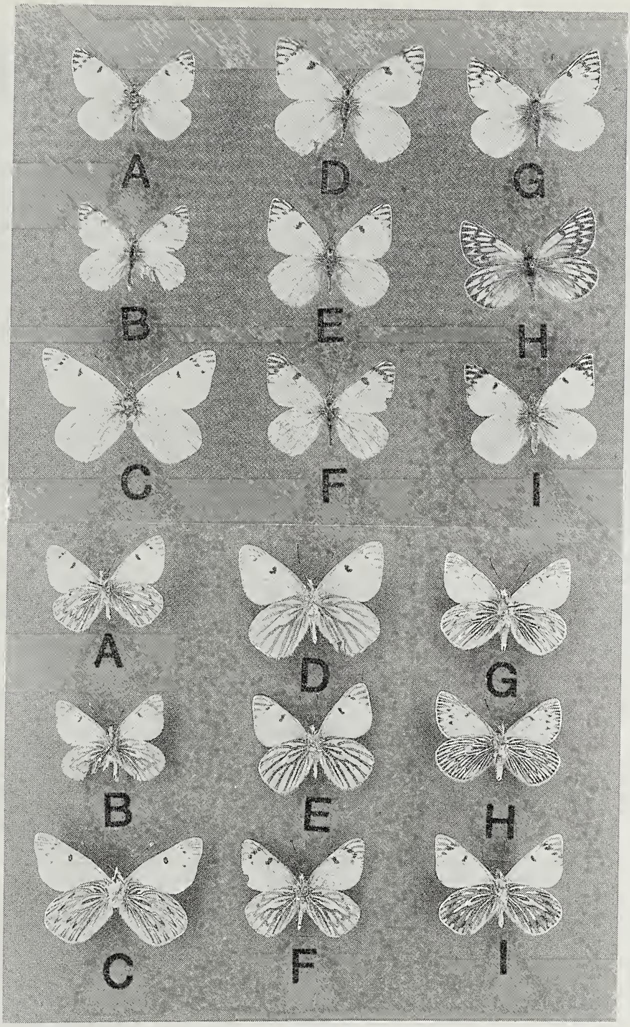


Fig. 18. Various *Hypsochila*. All males except H, female. A, *H. wagenknechti sulfurodice*, Chile, Mamiña, Tarapacá, 30.IX.1974 (J. Herrera). B, same, Tres Cruces, Jujuy, 7.II.1984. C, *H. argyrodice*, Fitz Roy, Santa Cruz, 11.II.1979 (DE). D, E, F all Cerro Amarillo, Jujuy, 4.I.1980 (RE): D and E resemble *H. galactodice*, F resembles *H. w. sulfurodice*. G, H, *H. microdice*, Río Grande, Tierra del Fuego, 25.XI.1988. I, *H. w. wagenknechti*, aberration, Arroyo de Agua Negra, San Juan, 3.XI.1988 (first brood).

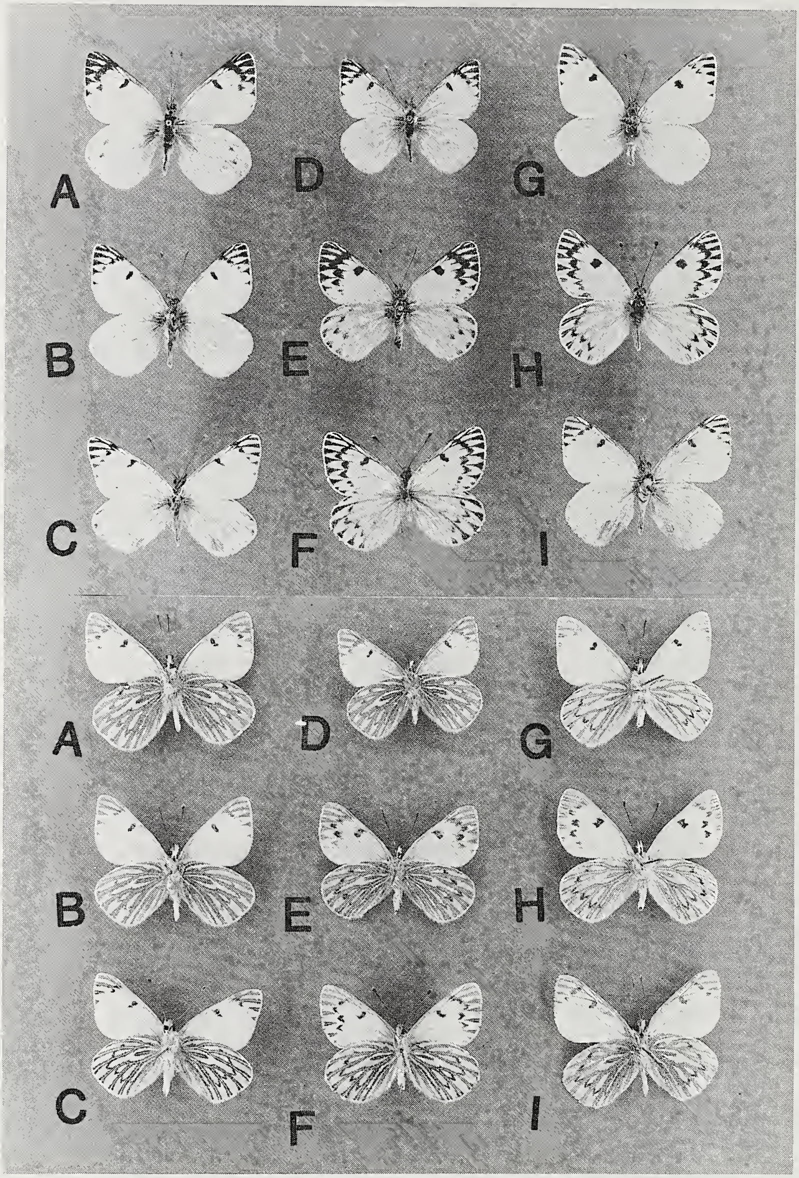


Fig. 19. Various *Hypsochila*. A, B, C, D, G, I males; E, F, H females. A, *H. w. wagenknechti*, Chile, Los Libertadores, Prov. Los Andes, 27–28.I.1983 (second brood). B, E, same, Arroyo de Agua Negra, San Juan, 3.XI.1988 (first brood). C, F, *H. galactodice*, Esquel, Chubut, 17.XI.1988 (first brood). D, *H. w. wagenknechti*, Chile, La Parva, Prov. Santiago, 24.XI.1982 (first brood). G, H, *H. galactodice*, bred without diapause ex Esquel, Chubut, emerged 23–25. XII.1988. I, Species uncertain (*wagenknechti*? *galactodice*?), Cordón del Viento, Neuquén, 28.I.1985.

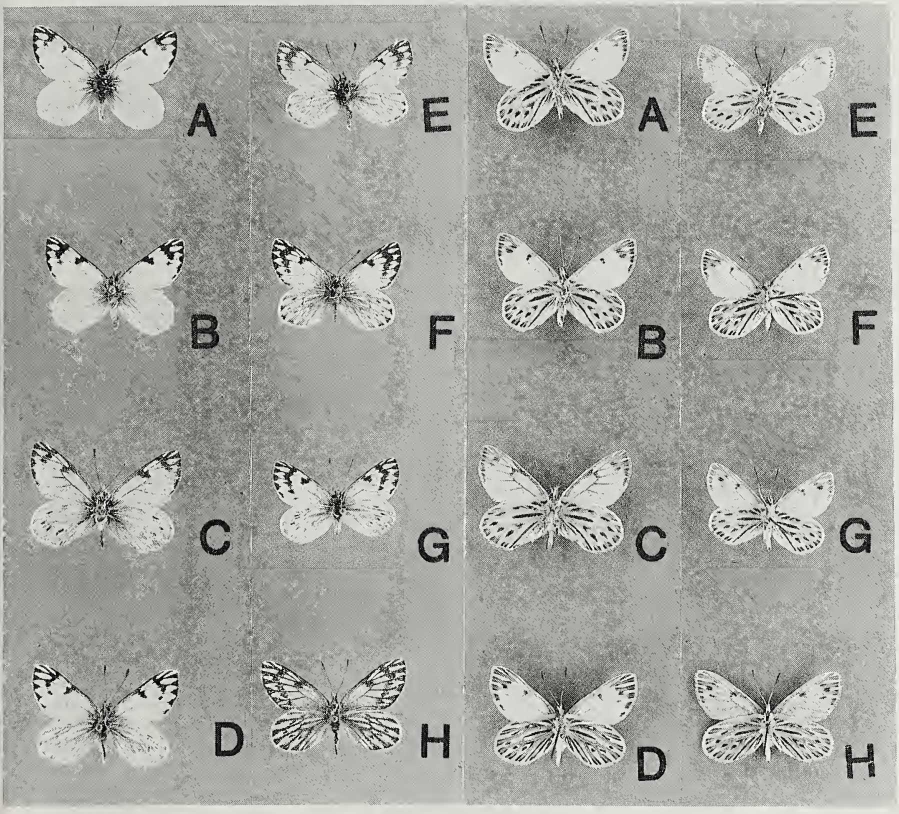


Fig. 20. *Phulia nymphula.* A–D, males; E–H, females. A, B, E, F, G, all Paso Bermejo, Mendoza, 31.X–1.XI.1988 (1st brood; G is a white, male-like female, E is phenotypically similar to *Pierphulia* above). C, Cordón del Viento, Neuquén, 28.I.1985. D, H, Esquinas Blancas, Jujuy, 7.II.1984. D and H are quite typical of *puna* specimens, with longer wings, heavier female pattern, and a more straw, less pinkish color below.

Fig. 21. Mosaic gynandromorph *Phulia nymphula* from Paso Bermejo, Mendoza, 31.X–1.XI.1988. The left FW is apparently all male, the right FW all female, both HW mostly female (left 7/8, right 2/3); the external genitalia are malformed and intermediate. This is the first gynandromorph reported in nature for any Andean pierine.

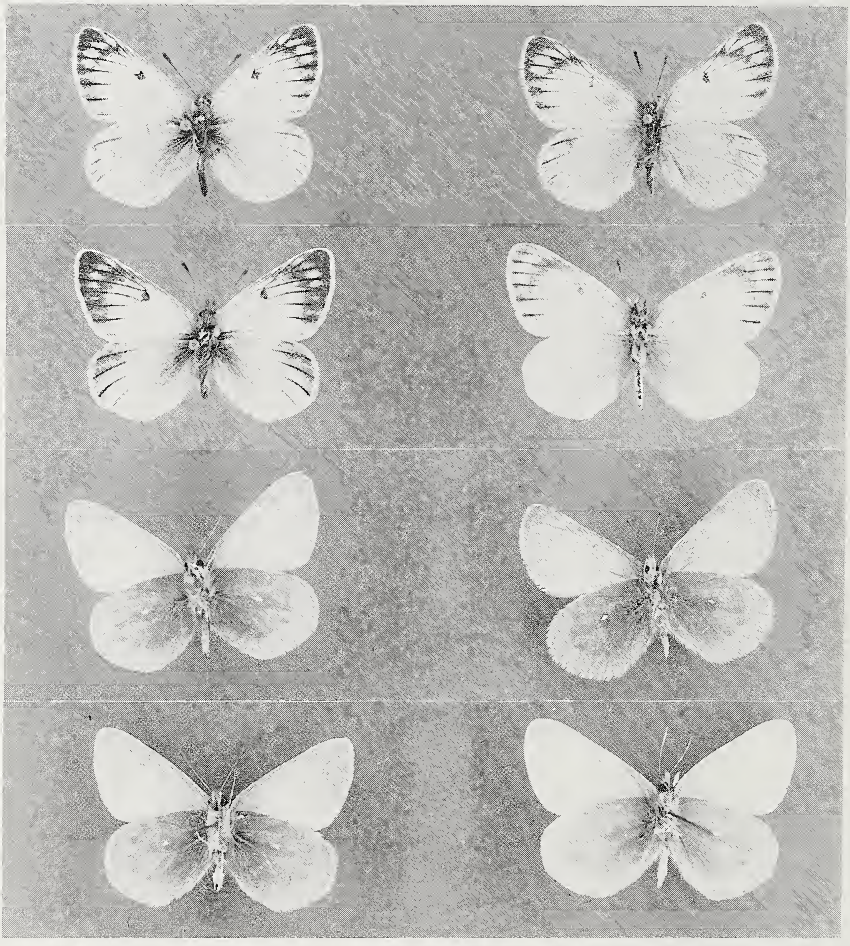


Fig. 22. *Colias flaveola* from Arroyo de Agua Negra, San Juan, 3.XI.1988, males at left in both views.

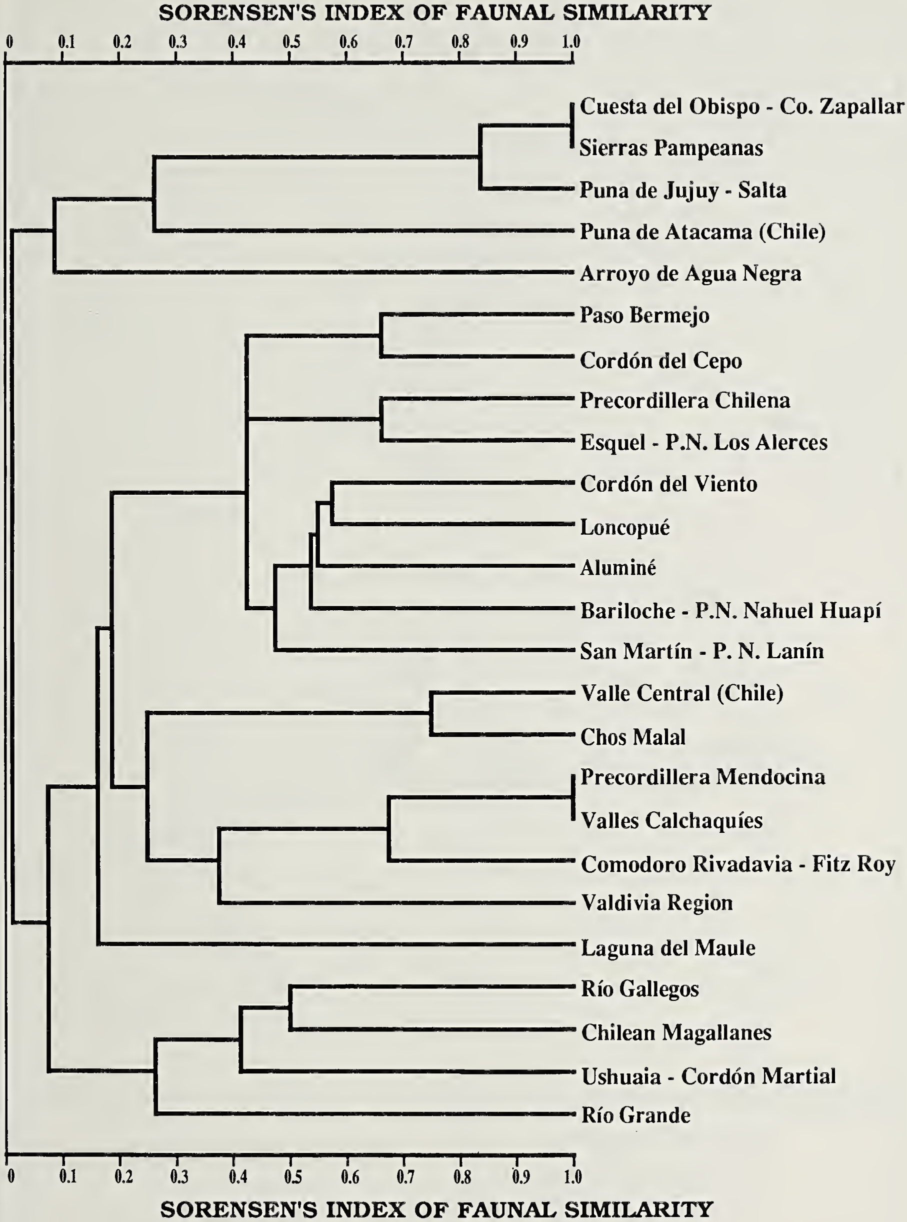


Fig. 23. Dendrogram generated by cluster analysis (UPGMAA) showing relationships among selected faunas compared in Tables 1–3. (For purposes of calculation, species and subspecies were treated equally.)

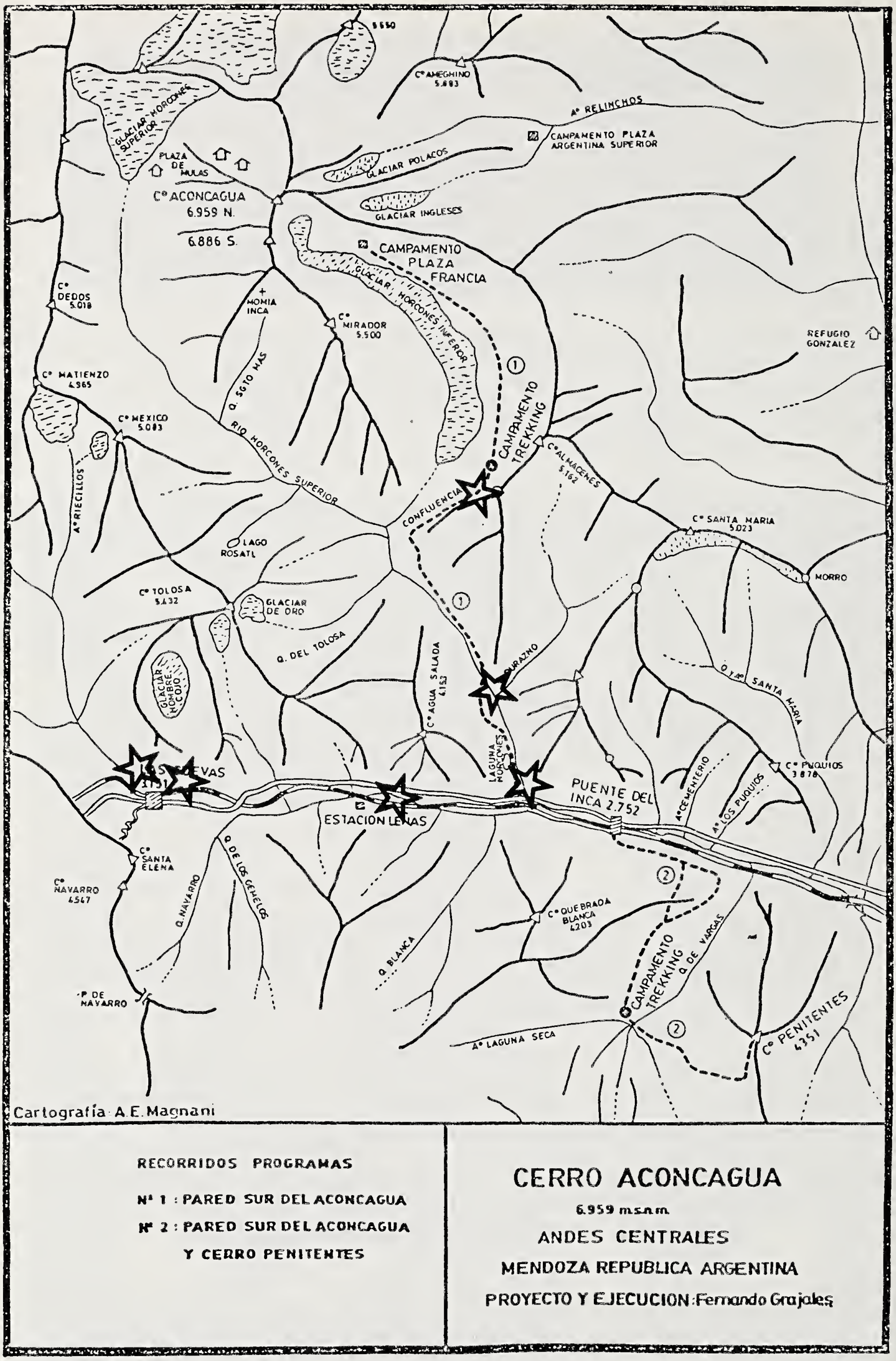


Fig. 24. Argentine sketch map of the Parque Provincial Aconcagua, Mendoza, showing (stars) locations of known suitable *vegas* for the occurrence of *Colias mendozina*. Actual captures are from Quebrada de los Horcones, just NW of Puente del Inca near the middle of the map.

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IN THIS ISSUE

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The Zoogeography and Systematics of the Argentine Andean and Patagonian Pierid Fauna — 137
Arthur M. Shapiro

COVER ILLUSTRATION: Female *Tatochila m. mercedis* ovipositing on high-altitude rosette Crucifer near the Argentine-Chilean border in the Cordillera Real. Photograph by Arthur M. Shapiro.

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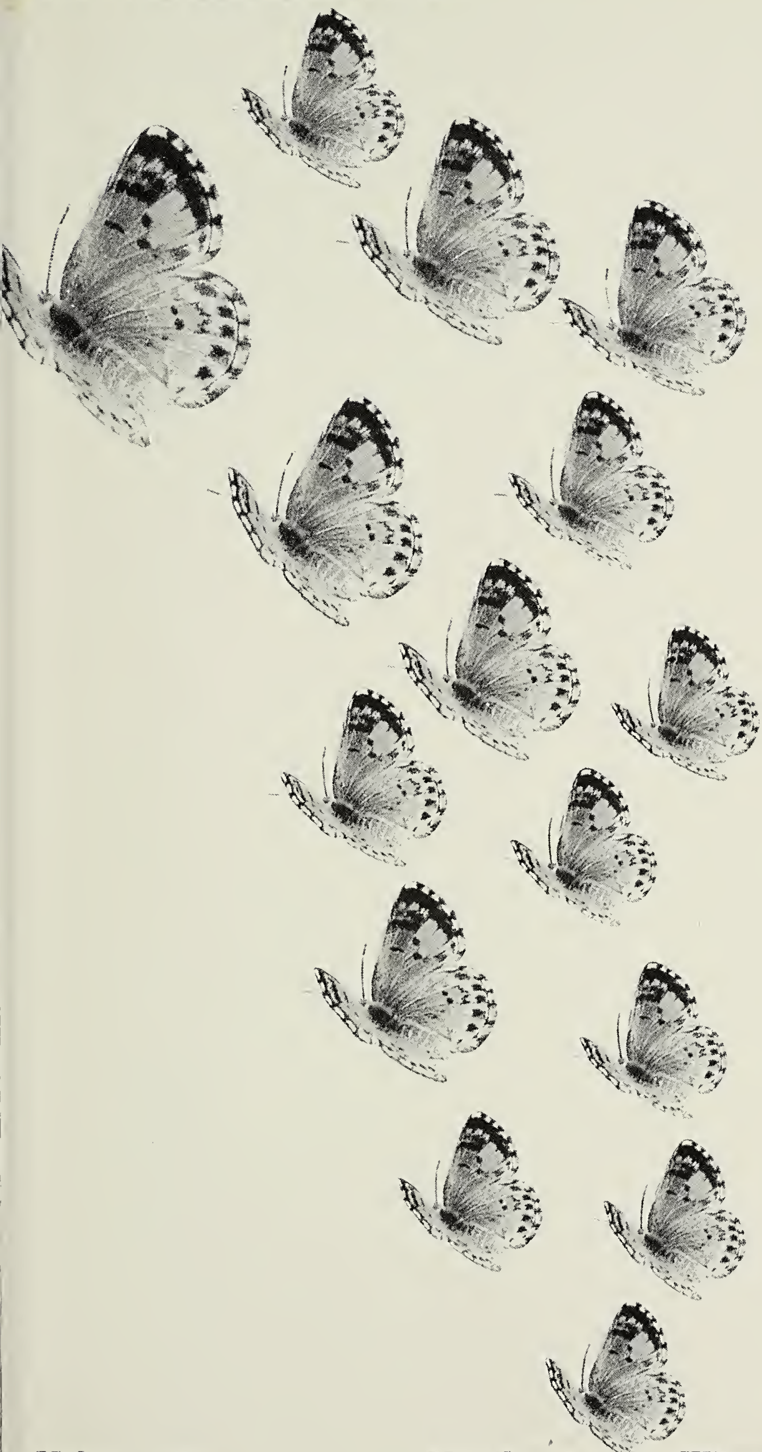

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European and North West African Lycaenidae (Lepidoptera) and their associations with ants

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Abstract. The information about ant-associations of European and North West African lycaenid caterpillars is summarized. A tentative classification of the different degrees of myrmecophily is proposed. More than 75 % of the species considered are myrmecophilous. In the Polyommatini, even more than 90 % are ant-associated. An apparent correlation between the ant-association of lycaenids and their systematic position is discussed. This is contradictory to a recent work that suggested a much lower proportion of myrmecophilous species in the Western Palaearctic region and rejected any connections between lycaenid phylogeny and myrmecophily.

Introduction

The association of lycaenid larvae and ants, termed myrmecophily, has been the subject of extensive research. During the last decade, in particular, a number of papers concerned with the physiology, ecology, and evolution of lycaenid myrmecophily have been published (e.g. Pierce, 1983, 1985, 1987; Pierce and Mead, 1981; Pierce and Eastseal, 1986; Henning, 1983 a & b; Cottrell, 1984; Fiedler and Maschwitz, 1988 a & b, 1989 a & b). However, a comprehensive compilation of all information regarding lycaenid myrmecophily from a single biogeographical area has not yet been undertaken. In 1969, Malicky listed the ant-associations of European species recorded until then, but in the past 20 years considerable progress has been made in the investigation of larval life-histories, adding numerous records of ant-larvae associations. Thus, it seems justified to summarize the current knowledge of Western Palaearctic lycaenids and their ant-associations, to point out the still significant gaps in our knowledge, and to discuss the results in the light of the recent research on myrmecophily and, in particular, the biogeographical and evolutionary hypotheses of Pierce (1987).

In the present paper I have attempted to gather all available, but scattered information on ant-associations and the presence of myrmecophilous organs in European and North West African lycaenid species. Important sources of data were the most useful review papers of Warnecke (1932/33), Hinton (1951), Malicky (1969), and Kitching and Luke (1985). Further information was derived from the books of Weidemann (1986, 1988) and SBN (1987), but special efforts were devoted to sample data from original sources, e.g. numerous journal papers and observations of several colleagues. Despite my efforts to approach completeness, the

following list is certainly still far from being complete, and further additions will be welcome.

Methods

In the present study I have considered all lycaenid species known from Europe and North West Africa north of the Sahara desert as listed in Higgins and Riley (1978) and Kudrna (1986), and the available information regarding the presence of myrmecophilous organs and ant-associations was compiled. The systematic arrangement basically follows Scott and Wright (1990). Thus, the "Theclinae" sensu Eliot (1973) are regarded as paraphyletic and are replaced by the (more likely monophyletic) tribes Aphnaeini, Theclini, and Eumaeini. The former subfamilies Lycaeninae and Polyommatinae are likewise downgraded to tribal level, i.e. Lycaenini and Polyommatini, respectively. The phylogenetic relationships of these tribes to each other, as well as to the other lycaenid subfamilies (Poritiinae including Liptenini; Miletinae including Liphyrini; Curetinae) are not yet sufficiently established. Indeed, some of the taxa considered here strongly need further confirmation as monophyletic groups. Because a more satisfactory phylogenetic higher classification of the Lycaenidae is not yet available, the arrangement adopted here is necessarily tentative.

The Riodinidae (with the single European species *Hamearis lucina* L.) are treated as a separate family, their associations with ants being based on the convergent evolution of structurally different ant-organs (see Cottrell, 1984; DeVries, 1988 & 1990) which occur only in the most apomorphic tribes Eurybiini, Lemoniini, and Nymphidiini (Harvey, 1987). It is important to stress that riodinid myrmecophily should be discussed as a phylogenetically separate and functionally convergent phenomenon when compared with ant-associations of the Lycaenidae (DeVries, 1990).

Nomenclature and taxonomy largely follow Kudrna (1986) with only minor deviations. The subgenera of the genus-groups *Plebejus* and *Polyommatus* are basically treated as in the paper of Zhdanko (1983). Exceptions are the taxa *Eumedonia* (here included in *Aricia*), *Lysandra* (including *Plebicula* sensu Higgins and Riley, 1978) and *Meleageria* (both as subgenera of *Polyommatus*). The generic classification within most groups still strongly requires a phylogenetic analysis.

The species concept is in most cases adopted from Higgins and Riley (1978) and Kudrna (1986). Exceptions are, for example, the *Plebejides* and *Lysandra* groups (after Schurian, 1989, Bálint & Kertész 1990) and a few taxa of *Agrodiaetus*. In the latter subgenus, a number of taxa has been described from the Mediterranean area solely based on chromosome studies, but their taxonomic status needs further investigations. In general, subspecies and local forms are not considered separately, but highly isolated endemic forms (e.g. from several southern European mountain areas) are treated as distinct species (instead of vicariant subspecies) because of their genetic separation.

Based on the records available, I have tentatively assigned the degree of larval myrmecophily to each species where possible. This assignment is based primarily on field records, laboratory experiments are considered only exceptionally. The scoring is as follows:

0: not ant associated: **myrmecoxenous**.

1: very few ant-associations reported, stable ant-associations formed only exceptionally: **weakly myrmecophilous**.

2: a varying proportion of larvae attended by ants, intermediate between 1 and 3: **moderately myrmecophilous**.

3: most if not all mature larvae ant-associated: **steadily myrmecophilous**.

4: larvae dependent on ants as commensales (*Cigaritis*) or parasites (*Maculinea*): **obligately myrmecophilous**.

Usually the scorings in Table 1 refer to the larvae. Where the pupae are known to have a different stage of myrmecophily, this is indicated separately.

The presence of larval myrmecophilous organs is represented in Table 1 as follows: two asterisks (**) indicate a complete set of ant-organs (a dorsal nectary organ (DNO) plus a pair of eversible tentacle organs (TOs)); one asterisk means that only a DNO is present (sometimes only rudimentary, e.g., *Callophrys*: Fiedler 1990b). Species without an asterisk possess only pore cupola organs (PCOs) (see Cottrell, 1984 and Fiedler, 1988 for terminology, details and references).

When the figures indicating the degree of myrmecophily, or the asterisks referring to the equipment with ant-organs are bracketed, the respective assignments are hypothetical. In these cases the assignment is based on the status of closely related species (example: in *Agrodiaetus* the early instars of only a few species are well-known and all are highly ant-associated; judging from the close affinity between these taxa, it seems very likely that all *Agrodiaetus* caterpillars possess a full set of myrmecophilous organs and are steadily myrmecophilous).

Where possible from the records available, the ant genera and/or species involved in myrmecophilous interactions are listed. It has to be emphasized that many determinations were not checked by ant specialists, thus several old records are reliable only on genus level. For example: *Lasius "niger", "alienus"*, and *"flavus"* all are complexes of several closely related ant species which are nearly indistinguishable for the non-myrmecologist (e.g. Seifert, 1988 and pers. comm.). The term "indet." means that ant-associations have been observed but the ants involved were not determined. A question mark (?) indicates that ant-associations are likely, but no certain information is available. The dash (–) means that ant-associations have never been reported for the respective lycaenid species.

Regarding the sources of data, I have listed the review papers and books as references where appropriate to faciliate use. Special journal articles and personal communications are only cited when the information in the major references is incomplete or even incorrect. Purely descriptive papers (e.g. rearing records) are excluded except when they yield the only information about the presence or absence of ant-organs. Similarly, laboratory observations on myrmecophily are only considered when no sufficient field data are available. For most species the knowledge is still far from being complete. In several cases (species from Southern Europe) only information from outside Europe (e.g. Africa) is available, and for a few taxa there is no information regarding the larval biology at all (see footnotes to Table 1).

The information sampled in Table 1 is used for a quantitative analysis to determine the number and proportion of myrmecophilous species in the Western Palaearctic fauna. In Table 2a only those species are considered where appropriate information on the larval biology, including direct (positive or negative) evidence concerning myrmecophily, is present. In Table 2b, in addition, all species are included where at the current stage of our knowledge a reasonable

hypothetical assignment can be made (based on the presence of myrmecophilous organs and/or the state of the closest relatives). In accordance with experimental work (e.g. Fiedler and Maschwitz, 1989a, Fiedler, 1990a), the presence of a functional DNO is considered to indicate a facultative ant-association at least, while in species without ant-organs (DNO and TOs) such associations are supposed to be non-existent or weakly developed at most.

Results and Discussion

In Table 1 the European and North West African lycaenid species are listed together with the information about their ant-associations. The first column contains the species name, the second column gives the tentative assignment of the degree of larval myrmecophily. In the third column the ant genera or species involved are given, and the last column contains the source of data. Table 2 summarizes the absolute numbers and percentages of myrmecophilous species.

It is apparent from the Tables 1 and 2 that, in the Western Palaearctic region, the vast majority (more than 75 %) of lycaenid species are myrmecophilous at least towards the end of the larval stage. This conclusion can be drawn from either direct evidence (Table 1, 2a) or hypothetical assignments (Table 2b), which both yield almost identical figures. Thus there is a marked contrast to the results of Pierce (1987), who stated that only 30 % of the European species (32 % of the genera) are myrmecophilous. The reason for this difference is the incomplete evaluation of literature records: Pierce's data are derived solely from the review papers of Malicky (1969), Kitching and Luke (1985), and identification guides like Higgins and Riley (1978).

On the grounds of her data, Pierce (1987) concluded that there is a difference in the proportion and obligateness of ant-associated lycaenids between the northern and southern hemisphere, the latter having 70-90 % myrmecophilous species, the former only 20-40 %. From the results presented here it becomes obvious that this disparity does not exist for, at least, the proportion of myrmecophily in Europe; instead, the figures in Table 2 are close to those for the southern hemisphere given by Pierce. In Japan, the proportion of myrmecophilous species is about 56 %, but this rather low figure is mainly due to the preponderance of myrmecoxenous Thecliti there (Fiedler, 1990 a). The systematic structure of the Japanese lycaenid fauna is thus not representative for the whole Eastern Palaearctic region. From the Nearctic region a considerably smaller proportion of myrmecophilous species has been definitely recorded (about 30 %: Fiedler, 1990 a), but this awaits further confirmation (see Ballmer and Pratt, 1988).

Whether the degree of myrmecophily does show a north-south disparity remains to be clearly demonstrated. In the Western Palaearctic region only few species in the genera *Maculinea* (Thomas et al., 1989) and *Cigaritis* (Rojo de la Paz, 1990) are known to be obligately myrmecophilous. Recent observations on *Plebejus argus* and *P. (Lycaeides) idas* in

Europe, however, suggest that both are obligatorily and specifically associated with certain ants (*Lasius* species from the *niger* and *alienus* groups in the case of *P. argus*, species of the *Formica cinerea* group in the case of *P. idas*; see Mendel and Parsons, 1987, Jutzeler, 1989c & d, 1990, Ravenscroft, 1990). In the tropics detailed studies on lycaenid-ant interactions are still rather sparse. Only from South Africa (e.g. Clark and Dickson, 1971, Henning, 1983a, b) and from Australia (Common and Waterhouse, 1981) sufficient information is present on a larger number of species, while in South Asia most records are merely anecdotal (cf. Corbet and Pendlebury, 1978), and the life-histories of Neotropical Lycaenidae are largely unknown. The data from South Africa indeed suggest a high proportion (about 50 %) of obligatorily myrmecophilous lycaenid species, largely due to the great diversity of the tribe Aphnaeini (*Aloeides, Poecilmitis* etc.) and the genus *Lepidochrysops* in Africa. In Australia, the *Lucia* and *Zesius* sections of the Theclini contain a rather high number of obligate myrmecophiles (> 30 % of all Australian lycaenids), whereas the situation in South Asia appears to be intermediate (10-20 % obligate myrmecophiles; Fiedler, 1990 a). Thus, the current stage of our knowledge does not conclusively support Pierce's hypothesis concerning the general north-south disparity in the obligateness of lycaenid-ant interactions. Rather the high proportion of obligate myrmecophiles among the lycaenids of South Africa and Australia may reflect the peculiar history of the latter 2 areas (Fiedler, 1991).

In Europe, most lycaenids are associated non-specifically with a variety of ant species, often from different subfamilies. Only about 10 species from the genera *Cigaritis, Maculinea* and *Plebejus* maintain species- or at least genus-specific relationships with ants (see above). As was already pointed out by Malicky (1969), the dominance structure of the ant fauna in the larval habitats is decisive for which ant species actually tends a lycaenid caterpillar. In fact, members of any ant genera that maintain trophobiotic relationships with other organisms producing nutritive liquids (e.g. homopterans, myrmecophytes) are likely to attend myrmecophilous lycaenid larvae (DeVries, 1991). Because of the general dominance of Formicinae ants in temperate regions (e.g. Seifert, 1986; Fellers, 1987, 1989) it is not surprising that the dominant trophobiotic formicine genera *Lasius* (recorded with 23 lycaenid species), *Formica* (14 species), *Camponotus* (10 species) and *Plagiolepis* (10 species), as well as *Tapinoma* (Dolichoderinae; with 12 lycaenid species), *Myrmica* (Myrmicinae; 20 species) and *Crematogaster* (10 species) are mentioned most often in Table 1.

Although the higher classification of the Lycaenidae is not yet resolved, another pattern is apparent from the results above: There is a strong correlation between systematic position and myrmecophily (Fiedler, 1990a). Most members of the Lycaenini, for example, have no ant-associations, presumably due to the absence of a dorsal nectary organ. Only for one European species, *Lycaena dispar*, there exist old records of

ant-associations, while the remaining 12 European species appear to be myrmecoxenous. In North America only 4 out of 15 species of the genus *Lycaena* are with certainty known to associate with ants with the help of specialized dendritic setae (Ballmer and Pratt, 1988). Ant-associations are unknown from African and New Zealand *Lycaena* (Clark and Dickson, 1971, Gibbs, 1980), from Asian *Heliophorus* (Eliot, pers. comm.) and from Papuan *Melanolycaena* (Sibatani, 1974). Thus, the Lycaeninae as a whole seem to be a myrmecoxenous group with only few secondary exceptions.

The Polyommatini show the reverse pattern: nearly all European species are ant-associated (Table 1), the only exceptions being the subgenera *Agriades* and *Vacciniina*. Both occur in arctic or alpine tundra, or wet boreo-montane bogs with limiting nutritional resources and few ant species present. The Polyommatini of Africa, Australia, and North America also contain a large number of myrmecophilous species (e.g. Clark and Dickson, 1971, Common and Waterhouse, 1981, Ballmer and Pratt, 1988) with rather few exceptions (e.g. desert species, lycaenids with endophytic larvae). Thus, the Polyommatini are basically ant-associated and reductions of myrmecophily (and ant-organs) have occurred in only a few species that occur where the ecological conditions did no longer favor the symbiosis with ants.

The predominantly African tribe Aphnaeini is another strongly myrmecophilous group: the high proportion of obligately myrmecophilous species in South Africa is mainly due to the Aphnaeini genera *Aphnaeus, Apharitis, Spindasis, Aloeides, Phasis, Poecilmitis,* and the polyommatine genus *Lepidochrysops* (Clark and Dickson, 1971; Claassens and Dickson, 1980). The only representatives of the Aphnaeini in the Palaearctic region (genus *Cigaritis*) are specifically associated with ants of the myrmicine genus *Crematogaster* (Rojo de la Paz, 1990).

The remaining and rather heterogeneous tribes Theclini and Eumaeini show different pictures. The Theclini contain a large number of ant-associated species in South Asia, Africa, and Australia (Clark and Dickson, 1971, Corbet and Pendlebury, 1978, Common and Waterhouse, 1981). The 3 European species as well as the 2 North American members of this tribe, however, belong to the mainly Sino-Oriental subtribe Thecliti, and this whole subtribe has apparently reduced its ant-associations. Possibly the Thecliti (as the temperate-zone sister-group of the Arhopaliti, a basically Oriental ant-associated lineage) reduced their myrmecophily when adaptaing towards temperate regions. In South East Asia and Australia, the Theclini subtribes Luciiti, Zesiiti, Ogyriti, and Arhopaliti are predomionantly myrmecophilous, including a number of obligately ant-associated species (e.g. Common and Waterhouse, 1981, Fukuda et al., 1984, Fiedler, 1990a).

The tribe Eumaeini sensu Scott and Wright (1990) is the largest of the whole family Lycaenidae. Myrmecophily and myrmecophilous organs are known from its subtribes Amblypodiiti, Catapaecilmatiti, Loxuriti,

Iolaiti, Deudorigiti, and Eumaeiti (Fiedler, 1990a). In Europe there are only a few representatives of the genus *Tomares* and the subtribe Eumaeiti. The *Tomares* species possess a complete set of ant-organs and are facultatively ant-associated. *Tomares* belongs to the Deudorigiti (Eliot, pers. comm.) which subtribe contains a number of myrmecophilous species in the tropics (e.g. Clark and Dickson, 1971).

The Eumaeiti are most diverse in America (Eliot, 1973) including the species-rich genera *Callophrys, Strymon, Satyrium*. In the Palaearctic region, comparatively few species (< 60) of the genera *Satyrium* s. l. and *Callophrys* s. l. occur (Bridges, 1988). Within the genus *Satyrium* there appears to be a marked tendency to reduce ant-associations, and this is even more pronounced in *Callophrys* where only very few species have been found to be tended by ants. Interestingly, both genera lack the tentacle organs (Ballmer and Pratt, 1988), and the dorsal nectary organ ("honey gland") - though present - does not secrete nutritive liquids in some species (e.g. *Callophrys rubi*, Fiedler, 1990b). Hence, the Eumaeini of the temperate regions seem to be a tribe with a basically low level of myrmecophily and a high tendency to further reduce ant-associations and the related organs. Unfortunately the current knowledge of the biology of neotropical Eumaeiti is still too fragmentary to support further interpretations. The ecological regimes selecting for the parallel reduction of myrmecophily in the Theclini and Eumaeini are not as clear as in the Polyommatini. Possibly the preference for rather nutrient-poor foodplants of the families Fagaceae, Betulaceae, Salicaceae and others may play a role, together with the generally lower diversity and abundance of ants in temperate woodlands (Jeanne, 1979), resulting in a lower chance of maintaining stable trophobiotic associations there. Most of the Palaearctic Polyommatini species, in contrast, occur in open habitats which support a more diverse ant fauna (Seifert, 1986). Clearly further studies are required on this interesting evolutionary feature.

It is now relevant to asses the importance of these results with respect to the biogeography of lycaenid myrmecophily. Apparently the systematic composition of the lycaenid fauna of the biogeographical regions largely influences the proportion and obligateness of myrmecophily. The lycaenid fauna of Europe, for example, is predominated by species of the Polyommatini (72 %), resulting in a high proportion of (at least facultatively) ant-attended lycaenids. The Lycaenidae fauna of North America, in contrast, contains a higher percentage of Eumaeiti and Lycaenini species (67 % of the resident species). Not surprisingly, the proportion of myrmecophily is lower. Among the African lycaenids, two thirds of the fauna belong to the Aphnaeini, Old World subtribes of the Eumaeini, and Polyommatini: Most of these species are myrmecophilous. The remaining third are species of the Poritiinae whose larvae in most cases do not maintain close ant-associations (Clark and Dickson, 1971).

Thus, contradictory to the conclusions of Pierce (1987: "The distribution of ant association within the Lycaenidae is independent of phylog-

eny"), this study suggests a high correlation between lycaenid phylogeny and the evolution of myrmecophily. It also suggests that this systematic effect may significantly influence the biogeography of lycaenid-ant-associations. Notwithstanding the uncertainties of lycaenid systematics, a substantial discussion of the biogeography and evolution of lycaenid myrmecophily can hardly be realized without a phylogenetic approach. Much more work needs to be done on the higher classification of the Lycaenidae as well as in the description and analysis of larval life-histories and ant-associations in all biogeographical regions to confirm or reject the hypotheses given above. This paper is a first attempt to understand a small region (Europe), and is intended to stimulate broader and more thorough analyses.

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Table 1: List of species, degree of myrmecophily, and associated ants of European and North West African Lycaenidae and Riodinidae. Only field records are included except where stated otherwise (lab.). Further explanations see text and footnotes.

Species	Degree of myrmecophily	Ant species involved	Source of information
Riodinidae			
Hamearis lucina	0	—	Malicky 1969b (lab.) Fiedler 1990a
Lycaenidae			
Aphnaeini:			
Cigaritis zohra	4**	*Crematogaster laestrygon*	Rojo de la Paz 1990
C. allardi	3**	*Crematogaster auberti* *C. antaris* *C. scutellaris*	Rojo de la Paz 1990
C. siphax	(3/4**)	?	no record
C. acamas	4**	*Crematogaster* sp.	Larsen & Pittaway 1982
C. myrmecophila	4**	*Crematogaster auberti* *Cataglyphis bicolor?*	Hinton 1951
Lycaenini:			
Lycaena phlaeas	0	—	Kitching & Luke 1985
L. helle	0	—	SBN 1987
L. dispar[a]	0/1?	*Myrmica rubra*	Hinton 1951
L. virgaureae	0	—	SBN 1987
L. ottomanus[b]	(0?)	—	Elfferich, pers. comm. (lab.)
L. tityrus	0	—	SBN 1987
L. alciphron	0	—	SBN 1987
L. hippothoe	0	—	SBN 1987
L. candens	(0)	—	no record
L. thersamon	0	—	Larsen 1990
L. phoebus	0	—	Rojo de la Paz, pers. comm.
L. thetis	(0)	—	no record
L. ochimus	(0)	—	no record

Theclini:			
Thecla betulae	larva: 0/1 pupa: 3	*Lasius niger* (pupa)	Malicky 1969b, Kitching & Luke 1985, Emmet & Heath 1990
Laeosopis roboris	(1?)*	?	Agenjo 1963
Quercusia quercus	larva: 0/1 pupa: 2	*Lasius* sp.? (pupa)	Kitching & Luke 1985, Emmet & Heath 1990
Eumaeini:			
Tomares ballus	2**	*Plagiolepis pygmaea* + indet.	Chapman & Buxton 1919, Malicky 1969b, Jordano et al. 1990
T. mauretanicus	(2)**	?	Malicky 1969b
T. nogelii	3(**)	indet.	Hesselbarth & Schurian 1984
Callophrys rubi [c]	larva: 0/1* pupa: 2	??	Malicky 1969b, Fiedler 1990d, Emmet & Heath 1990
C. avis	(0)*	—	Dujardin 1972
Satyrium w-album	2*	indet.	Malicky 1969b, Kitching & Luke 1985, Schurian, pers. comm.
S. spini	2*	indet.	Malicky 1969b
S. ilicis	2*	*Camponotus aethiops*	Malicky 1969b, SBN 1987
S. esculi	2*	*Camponotus cruentatus*	Martín & Gurrea 1983
S. acaciae	0*	—	Schurian, pers. comm.
S. (Fixsenia) pruni	0	—	Kitching & Luke 1985
Polyommatini:			
Jamides section			
Lampides boeticus	2**	*Lasius niger* *Camponotus compressus* *C. cruentatus* *C. sylvaticus* *C. foreli* *Prenolepis clandestina* *Plagiolepis* sp. *Tapinoma melanocephalum*	Hinton 1951, Martín Cano 1984; Schurian & Wiemers pers. comm.
Leptotes section			
Leptotes pirithous [d]	2**	indet.	Hinton 1951, Clark & Dickson 1971, Munguira, pers. comm.
L. webbianus [e]	0/1**	?	Wiemers & Schurian, pers. comm. (lab.)
Castalius section			
Tarucus rosaceus	3**	*Plagiolepis pygmaea* *Camponotus sicheli* *Monomorium salomonis*	Chapman & Buxton 1919, Rojo de la Paz, pers. comm.
T. theophrastus	3**	indet.	Baz 1988
T. balkanicus	3*(*)	indet.	Wiltshire 1945, 1948
Zizeeria section			
Zizeeria knysna [d]	3**	*Tapinoma melanocephalum*	Warnecke 1932/33, Clark & Dickson 1971

Cupido section			
Everes argiades[d]	2**	indet.	Warnecke 1932/33
E. decoloratus	(2**)	?	no record
E. alcetas	(2)**	?	Elfferich, pers. comm. (lab.), Martín Cano 1982
Cupido minimus	3*	*Lasius alienus*	Malicky 1969b, Baylis & Kitching 1988
		Formica fusca	
		F. rufibarbis	
		Plagiolepis vindobonensis	
		Myrmica rubra	
C. lorquinii	3*	*Plagiolepis pygmaea*	Munguira & Martín 1989,
		Tapinoma nigerrimum	Munguira, pers. comm.
C. osiris	3**	*Lasius alienus* + indet.	Malicky 1969b, SBN 1987
Azanus jesous[d]	3**	indet.	Bell 1915, Clark & Dickson 1971
Lycaenopsis section			
Celastrina argiolus	2**	*Lasius niger*	Malicky 1969b, Harvey & Webb 1980, Kitching & Luke 1985, Emmet & Heath 1990
		L. alienus	
		L. fuliginosus	
		Camponotus japonicus	
		C. nearcticus	
		Formica subsericea	
		F. truncorum	
		Myrmica sp.	
Glaucopsyche section			
Glaucopsyche alexis	3**	*Lasius alienus*	Malicky 1969b, Martín Cano 1981, SBN 1987
		Formica pratensis	
		F. fusca	
		F. cinerea	
		F. nemoralis	
		F. subrufa	
		Camponotus aethiops	
		C. maxiliensis	
		Myrmica scabrinodis	
		Crematogaster auberti	
		Tapinoma erraticum	
G. melanops	3**	*Camponotus foreli*	Malicky 1969b, Martín Cano 1981
		C. cruentatus	
		C. micans	
		C. sylvaticus	
Maculinea arion	4*	*Myrmica sabuleti*	Thomas et. al. 1989
		M. scabrinodis	
M. teleius	4*	*Myrmica scabrinodis*	Thomas et al. 1989
		M. rubra	
		M. vandeli	
		M. sabuleti	
M. nausithous	4*	*Myrmica rubra*	Thomas et al. 1989
		M. scabrinodis	
M. alcon	4*	*Myrmica ruginodis*	Thomas et al. 1989
		M. rubra	
		M. scabrinodis	Liebig 1989 (lab.)
M. rebeli	4*	*Myrmica schencki*	Thomas et al. 1989, Jutzeler 1989b
		M. sabuleti	
		M. scabrinodis	
		M. sulcinodis	

Jolana jolas	2*	*Tapinoma erraticum* + indet.	Warnecke 1932/33, Malicky 1969b, Schurian, pers. comm.
Turanana panagaea[f]	?	?	no record
Pseudophilotes schiffermuelleri	(2)**	?	no record
Ps. baton	2**	*Lasius alienus* *Myrmica scabrinodis*	Malicky 1969b, Blab & Kudrna 1982
Ps. panoptes	(2**)	?	Nel 1982
Ps. barbagiae	(2**)	?	no record
Ps. abencerragus	(2**)	?	Martín Cano 1982
Ps. bavius	2*(*)	indet.	König 1988
Scolitantides orion	3**	*Camponotus vagus* *C. aethiops* *Tapinoma erraticum* + indet.	Chapman 1915c, Malicky 1969b
Polyommatus section			
Chilades trochylus[d]	3**	*Prenolepis* spp. *Pheidole quadrispinosa* *Iridomyrmex* sp.	Malicky 1969b, Clark & Dickson 1971, Wasserthal, pers. comm.
Plebejus argus	3/4**	*Lasius niger* *L. alienus* *Formica cinerea* ??	Kitching & Luke 1985, C. Thomas 1985, Mendel & Parsons 1987, Jutzeler 1989d, Ravenscroft 1990
P. vogelii	(3**)	?	no record
P. (Plebejides) martini	3**	*Crematogaster* sp.	Rojo de la Paz, pers. comm.
P. (P.) trappi	3**	*Formica lugubris* *F. lemani*	SBN 1987, Schurian & Jutzeler, pers. comm.
P. (P.) hespericus	3**	*Formica cinerea* *F. subrufa* *Plagiolepis pygmaea* *P. schmitzi* *Camponotus cruentatus* *C. foreli* *C. sylvaticus* *Crematogaster auberti*	Munguira & Martín 1989a, Munguira, pers. comm.
P. (P.) sephirus	3**	*Lasius* near *alienus*[g] *Formica pratensis* *Camponotus aethiops* *Tetramorium* near *caespitum*[g]	Bálint & Kertész 1990, own observations
P.(Lycaeides) idas	3/4**	*Formica cinerea* *F. selysi* *F. exsecta* *F. lemani* *F. pressilabris* *F. lugubris* *F. lefrancoisi* *F. fusca* ?	Malicky 1969b, SBN 1987, Jutzeler 1989c, 1990
P. (L.) argyrognomon	3**	*Lasius alienus* *L. niger* *Myrmica scabrinodis* *M. sabuleti*	Malicky 1969b, Blab & Kudrna 1982
P. (Kretania) eurypilus[f]	?	?	no record
P. (K.) psylorita	?	?	Hemmersbach 1989, Leigheb et al. 1990
P. (Vacciniina) optilete	0	—	Malicky 1969b

Polyommatus (Aricia)			
agestis	3**	*Lasius alienus*	Jarvis 1958/59, Kitching
		L. flavus	& Luke 1985, Emmet & Heath
		Myrmica sabuleti	1990, Schurian, pers. comm.
P. (A.) artaxerxes	3**	*Lasius* sp.	Malicky 1969b, SBN 1987
P. (A.) cramera	(3**)	?	no record
P. (A.) morronensis	3**	*Lasius niger*	Munguira & Martín 1988
		Crematogaster auberti	
		Tapinoma erraticum	
		T. nigerrimum	
P. (A.) nicias	(3)**	?	Warnecke 1932/33
P. (A.) anteros	(3**)	?	no record
P. (A.) eumedon	3**	*Myrmica* sp.	Malicky 1969b, Weidemann
			1986, SBN 1987, Schurian,
			pers. comm.
P. (Albulina) orbitulus	(2)**	?	Warnecke 1932/33, SBN1987
P. (Agriades) glandon	0	—	Malicky 1969b, SBN 1987
P. (A.) zuellichi	0	—	Munguira & Martín 1989
P. (A.) pyrenaicus	0	—	Chapman 1915a
P. (A.) dardanus	(0)	—	no record
P. (A.) aquilo	(0)	—	no record
P. (Agrodiaetus) damon	3**	*Lasius niger*	Warnecke 1932/33, SBN1987
		Formica pratensis	Malicky 1969b
P. (A.) iphigenia	(3**)	?	no record
P. (A.) dolus	(3**)	?	Martín Cano 1982
P. (A.) ainsae	(3**)	?	Martín Cano 1982
P. (A.) admetus	(3)**	?	Warnecke 1932/33
P. (A.) fabressei	(3)**	?	Martín Cano 1982,
			Munguira, pers. comm.
P. (A.) aroanensis	(3**)	?	no record
P. (A.) ripartii	3**	indet.	Munguira & Schurian,
			pers. comm.
P. (A.) humedasae	(3)**	?	Manino et al. 1987
P. (A.) thersites	3**	*Lasius alienus*	Rehfous 1954,
		Myrmica scabrinodis	Malicky 1969b,
		Tapinoma erraticum	Schurian, pers. comm.
P. (Cyaniris) semiargus	3**	*Lasius* sp.	Weidemann 1986
P. (C.) antiochena	(3**)	?	no record
P. (Lysandra) dorylas	3**	*Formica cinerea*	Rehfous 1954, Weidemann
		Lasius alienus	1986, SBN 1987
		Myrmica scabrinodis	
P. (L.) golgus	3**	*Tapinoma nigerrimum*	Munguira & Martín 1989b
P. (L.) nivescens	3**	*Tapinoma nigerrimum*	Munguira & Martín 1989b
P. (L.) atlantica	(3**)	?	no record
P. (L.) amandus	3**	*Lasius niger*	Hornemann, pers. comm.
P. (L.) escheri	3**	*Formica cinerea*	Chapman 1915b, SBN 1987,
		Myrmica specioides	own observ.
P. (L.) coelestina	(3**)	?	no record
P. (L.) coridon	3**	*Lasius niger*	Malicky 1969b, Kitching
		L. alienus	& Luke 1985, Fiedler 1987,
		L. flavus	Fiedler & Rosciszewski 1990,
		L. fuliginosus (??)	own observ.
		Plagiolepis vindobonensis	
		Formica rufa	
		Myrmica scabrinodis	
		M. sabuleti	
		M. schencki	
		Tetramorium caespitum	

P. (L.) hispanus	3**	*Plagiolepis pygmaea*	Maschwitz et al. 1975, Schurian, pers. comm.
P. (L.) albicans	3**	indet.	Schurian, pers. comm.
P. (L.) bellargus	3**	*Lasius alienus* *L. niger* *Plagiolepis pygmaea* *Myrmica sabuleti* *M. scabrinodis* *Tapinoma erraticum*	Malicky 1969b, Blab & Kudrna 1982, Kitching & Luke 1985, Jutzeler 1989e
P. (L.) punctiferus	3**	*Monomorium salomonis* *Crematogaster scutellaris*	Schurian & Thomas 1985
P. (Meleageria) daphnis	3**	*Lasius alienus* *Formica pratensis* *Tapinoma erraticum*	Schurian, pers. comm. & own obs.
P. (Polyommatus) icarus	2/3**	*Lasius alienus* *L. flavus* *L. niger* *Formica subrufa* *F. cinerea* ? *Plagiolepis pygmaea* *Myrmica sabuleti*	Malicky 1969b, Martín Cano 1984, Kitching & Luke 1985, SBN 1987, Jutzeler 1989d, Emmet & Heath 1990
P. (P.) eroides [f]	(3**)	?	no record
P. (P.) eros	3**	*Formica lemani* *Myrmica gallienii*	Jutzeler 1989a

Footnotes to Table 1:

[a] Only two (independent?) old records. In the extensive literature about this locally endangered species and in recent textbooks, no mention of any ant-associations is given. Like all other European *Lycaena* species for which appropriate information is available, *L. dispar* is probably not truely myrmecophilous.

[b] In laboratory experiments larvae of *L. ottomanus* were rather attractive to *Lasius niger* (Elfferich, pers. comm.).

[c] Only one very old and doubtful record of an ant-association; see Fiedler (1990b) for detailed discussion.

[d] Information concerning myrmecophily only available from outside Europe.

[e] Wiemers observed no ants attending young larvae of *L. webbianus* in the field. Schurian, during his laboratory rearing, offered mature larvae to German *Lasius niger*. First the larvae were rather unattractive, but after some time they were palpated by the ants and the DNO was active. Thus the species may be at least weakly myrmecophilous.

[f] Larval biology apparently unknown.

[g] The *Lasius* workers collected in Hungary belong to a new species of the *alienus* group with distinct pubescence on the clypeus (det. B. Seifert). The species will be described by Seifert. Workers of the *Tetramorium caespitum* complex from Hungary cannot be determined with certainty; sexuals would be required.

Table 2: Numbers and percentages of facultatively (category 1-3) or obligately (category 4) myrmecophilous, and of myrmecoxenous (category 0) lycaenid species in Europe and North West Africa. The first table (a) is based exclusively on certain field observations; species whose larval biology is insufficiently known are excluded. The second table (b) is based on all assignments given in Table 1 (i.e. degrees of myrmecophily deduced from the situation in closely related species or from the presence of larval ant-organs are included).

a)

Tribus	not ant-associated	facultatively ant-associated	obligately ant-associated
Aphnaeini	-	1	3
Lycaenini	9	-	-
Theclini	-	2	-
Eumaeini	4	6	-
Polyommatini	4	46	7
total: 82 (100 %)	17 (20.7 %)	55 (67.1 %)	10 (12.2 %)

b)

Tribus	not ant-associated	facultatively ant-associated	obligately ant-associated
Aphnaeini	-	2	3
Lycaenini	13	-	-
Theclini	-	3	-
Eumaeini	4	7	-
Polyommatini	6	73	7
total: 118 (100 %)	23 (19.5 %)	85 (72.0 %)	10 (8.5 %)

Detecting and recording the calls produced by butterfly caterpillars and ants

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Introduction

Chirping crickets, shrilling cicadas, and buzzing flies are familiar examples of how insects communicate with sound. Some sounds that are fundamentally important to insect communication systems may, however, be inaudible to the human ear because they are produced at very low amplitudes (Gogala 1985; Markl 1983). For example, low amplitude airborne sounds produced by wing-flapping may provide vital cues for species specific mate recognition in drosophilid flies (Hoy *et al.* 1988), or ants may use substrate-borne vibrations to recruit nestmates to a resource (Baroni-Urbani *et al.* 1988). Although many insects may produce low amplitude signals in their communication systems, investigators require instruments to detect them before they can be studied.

Studies concerned with low-amplitude insect sounds are generally conducted under laboratory conditions, and employ bulky and typically expensive detection and recording instruments. However, a particle velocity microphone and amplifier was recently designed by H. Bennet-Clark (1984) that is inexpensive, portable, and shows great promise as a tool for discovering and studying low amplitude insect sounds (e.g., Hunter 1987; Hoy *et al.* 1988). Using the Bennet-Clark particle velocity microphone I have been able to investigate the low amplitude, substrate-borne calls produced by riodinid and lycaenid butterfly caterpillars that form symbioses with ants (DeVries 1990; 1991). The purpose of this paper is to briefly describe my methods and experience in detecting and recording caterpillar and ant calls. My aim is to encourage a broader interest in the documentation and study of these calls - an area of biology where much remains to be explored.

The microphone and amplifier

Plans for the particle velocity microphone are found in Bennet-Clark (1984). My equipment was constructed by a friend, and modified from the original design in three ways: 1) the microphone itself is simply wrapped in flattened brass mesh (Fig 1a), 2) the monitor switch is spring loaded to the off position to save battery power, 3) the amplifier was fitted into an 140 x 75 x 32 mm aluminum box, and 4) the amplifier was fitted to accept both sizes of headphone jacks (Fig. 1b). To reduce bulk I use the

smallest set of headphones I could find - not the finest, but easy to pack. Thus, all the components of the amplifier and microphone are compacted for easy transport.

The recording stage

A serviceable recording stage can be made of two plastic Petri dishes with a 75 mm diameter circle cut from their centers (I have used both circular and rectangular types). The opposing bottoms of the Petri dishes are fitted together and held in place with 4 nylon screws and nuts, with a circular membrane of paper or transparent mylar sandwiched between the Petri dishes to provide the recording substrate (Fig 1a). The interchangeable nature of the membrane will allow recording of caterpillar calls as they are transmitted through different substrate materials (e.g., plant material, metal, paper, wood).

The stage is supported above a table by an adjustable set of gator-jaw clamps ('lab hands') that are available from laboratory or electronic supply houses. One of the gator jaws holds the stage, and the other jaw is used to hold the microphone against the membrane from below (Fig 1a&b). The user may want to make a more sophisticated recording stage set-up, but the one described here is inexpensive, compact, and durable in the field.

After connecting the microphone to the amplifier, detecting or recording caterpillar calls is done simply by placing a caterpillar on the membrane and allowing it to walk (be patient as it may take a few minutes) and monitoring the activity with the headphones. A pair of entomological forceps is useful for caterpillar manipulations. It is advisable to occasionally check that the microphone is placed correctly against the membrane (Fig.1a). The cleanest signals are obtained from lycaenid caterpillars that have been turned on their back - it eliminates the scratching sound produced by their tarsi gripping the membrane while walking. In the case of riodinid caterpillars, however, they quickly right themselves, and typically produce a lot of high frequency background noise.

Recording

A caterpillar call can be recorded on any tape recorder, but those with an adjustable gain yield the best results; the automatic gain on some tape recorders tends to increase unwanted noise on the tape. For my own work I use a Marantz PMD - 420 portable cassette recorder / player and record with high bias tape. While recording a call the tape recorder needs to be isolated from the surface where the recordings are being made. Otherwise the microphone will pick up the motor sounds of the tape recorder transmitted through the table. I do this by cushioning the recorder on a 50mm thick foam pad placed on a chair or box isolated from the table

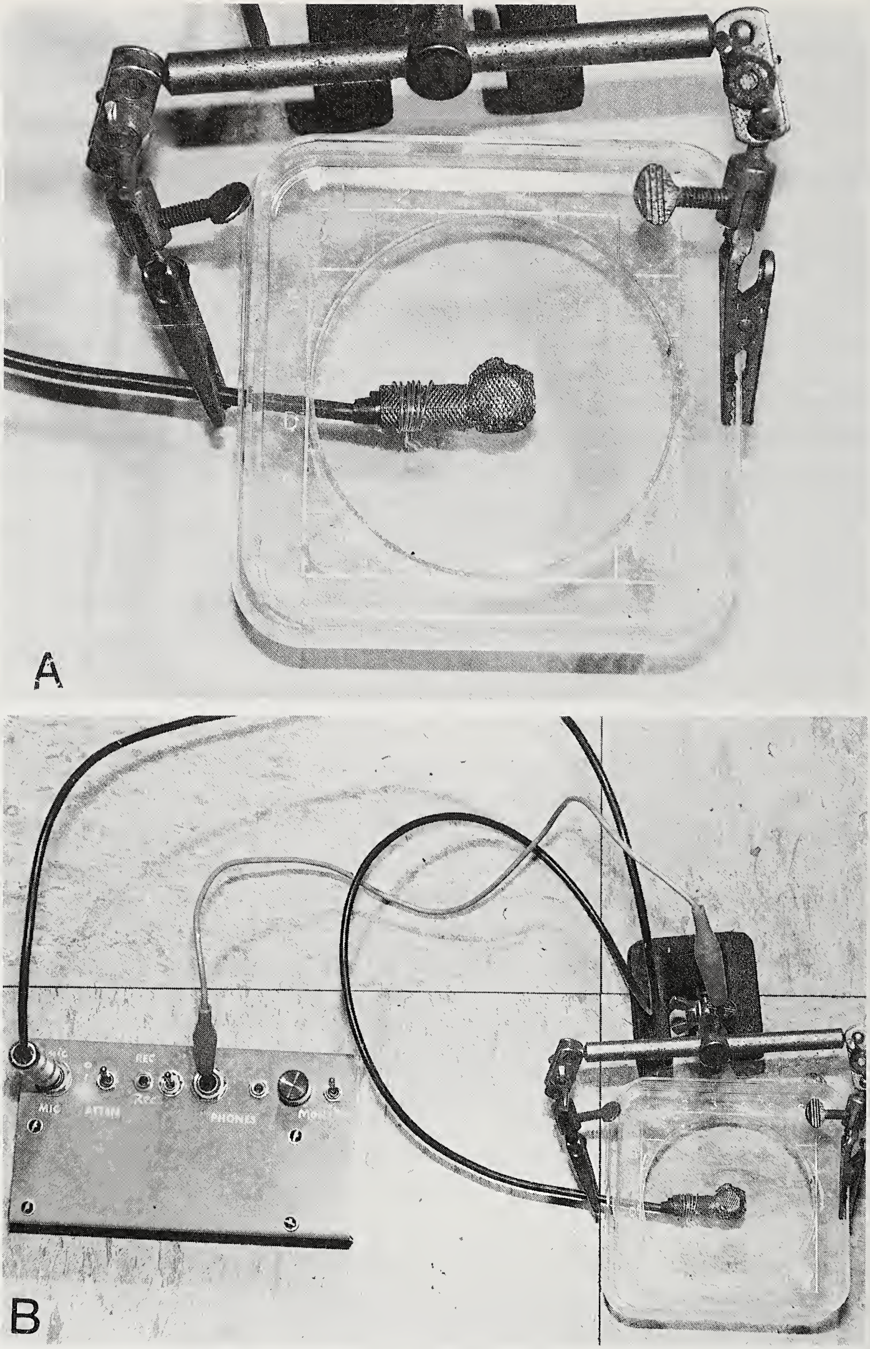

Figure 1: (A) Detail of the recording stage showing the gator-jaws, modified Petri dishes, transparent mylar membrane, and particle velocity microphone set up for recording caterpillar calls. (B) The amplifier, particle velocity microphone and recording stage set-up. The tape recorder and headphones are not connected. An idea of scale can be gained from the 31cm square floor tiles in background.

surface holding the microphone, amplifier, and recording stage. Secondly, recording extraneous substrate-borne signals generated from touching the table, the wires, or the amplifier (the microphone is *extremely* sensitive) may be minimized by placing the recording stage on a piece of foam rubber. Finally, a ground wire connected from the gator-jaw stage support to the amplifier will further reduce or eliminate line hum (Fig 1b).

Suggestions

A major consideration in obtaining good recordings is the inherent sensitivity of the equipment - ambient and incidental noise can be a problem. In many instances the user will find that in addition to caterpillar calls, the recordings will contain a seeming endless variety of other sounds: wind, rain, bird, insect, and frog calls, vibrations of people walking in the building, and perhaps most pestiferous, air conditioning devices and 50-60 cycle electrical hum. Thus, it is an advantage to record in a place where the investigator has some control over the environment. Generally I record late at night in a building where the inhabitants have left (or have been driven off) with the source of electricity shut off at the mains, and work with a battery-operated headlamp for illumination. Under conditions where the investigator cannot switch off the electrical mains, and experiences severe electrical interference, a copper mesh Faraday cage may be required. Field recordings are best made in a shed or tent during the day to minimize picking up the calls of nocturnal insects and amphibians on the recordings . However, at times rain, wind, and animal calls can be an annoying problem. Finally, keeping the 9 volt amplifier battery fresh will help reduce hum and flutter.

The silk normally laid down by walking caterpillars will build up on the membrane after extended use and allow caterpillars a firm grip on the substrate and generate unwanted noise as they walk. This source of irritating high frequency noise can be minimized or avoided by replacing or cleaning the stage membrane regularly . Using a mylar membrane will result in cleaner recordings because it minimizes the 'pops' produced by the caterpillar's tarsi hooking into the substrate, it is easily cleaned, and it has the added advantage of facilitating visual inspection of the microphone position (Fig 1b).

Ants are obviously important to the study of myrmecophilous caterpillars. Recording ant stridulations must be done in such a way as to avoid the excessive noise generated by the legs scrambling on the membrane. Some species will happily walk on the membrane and produce substrate stridulations or tapping. The industrious investigator may set up the microphone such that it contacts the side of a container holding a captive ant colony. However, the few times I tried this the typical frenzied activity of an ant colony came through loud and clear, thus making the recordings too cluttered for individual analysis. Holding ponerine or

myrmecine ants with forceps such that the legs are completely restrained (or removed), and touching the head or abdomen against the membrane gives good recordings of 'alarm' stridulations.

The equipment described here, the heart of which is the Bennet-Clark particle velocity microphone, has made it feasible for me to detect and record caterpillar, pupae, ant and beetle sounds in Ecuador, Panama, Costa Rica, Belize, the USA, Madagascar, England and Germany. As simple as it is, my equipment has endured a lot of field time under what may be termed 'not exactly sterile laboratory conditions', yet I have not experienced any appreciable problems with it. I hope that these methods described here will be expanded and improved upon through wider use in the investigations of low amplitude insect sounds. Certainly they have helped our understanding of the role of sound in caterpillar-ant symbioses.

Acknowledgements . Thanks to R. Hoy for giving me the reference for the particle velocity microphone, G. Raskin for building it, and a special thanks to H. Bennet-Clark for originally inventing it, and many pleasant chats during my visit to Oxford (Henry, I'm your greatest fan). This paper was encouraged by K. Fiedler, N. Greig, D. Grimaldi, U. Maschwitz, and D. Nash. I gratefully acknowledge the support of the MacArthur Foundation. This paper is dedicated to the memory of Dexter Gordon and Gordon B. Small - both of whom were experts in sound.

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Genetics and Biogeography of the *Oeneis chryxus* Complex (Satyrinae) in California

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Abstract. The nominal taxa *Oeneis ivallda* Mead and *Oe. chryxus stanislaus* Hovanitz are alpine butterflies endemic to the Sierra Nevada of California. The range of *Oe. c. stanislaus* is entirely contained within the range of *Oe. ivallda.* The two intergrade gradually in the north and abruptly in the south, and electrophoretic-genetic analyses fail to demonstrate any interruption in gene flow between them. This is consistent with the interpretation that *ivallda* and *stanislaus* are forms of a single species, and we recommend they be classified as subspecies of *Oe. chryxus* Doubleday and Hewitson pending comparisons with Rocky Mountain *Oe. chryxus chryxus*. Hovanitz's (1940, Ecology 21:371) hypothesis that the color morphs are maintained by selection for crypsis breaks down in the northern Sierra, where the pale *ivallda* morph is often found on dark substrates.

The peculiar distribution of these taxa suggests a double invasion of the Sierra, with *stanislaus* having arrived secondarily from the east across the Great Basin. We discuss the plausibility of the easterly colonization route, which remains controversial in the botanical literature. Further genetic investigation of the *chryxus* complex may provide a definitive test of this hypothesis.

Introduction

Oeneis ivallda Mead, a pale, sometimes nearly white Satyrine butterfly ranging from Nevada to Inyo and Tulare Cos. in California, is the only truly endemic butterfly to reach both the north and south alpine limits of the Sierra Nevada. Its biogeographical relationship with what is presently called *Oeneis chryxus stanislaus* Hovanitz has posed an evolutionary problem now recognized for over 50 yr. This relationship bears in turn on the origin of the alpine biotic community in this mountain range. *Oe. chryxus stanislaus* was described by Hovanitz (1937) from Sonora Pass, Alpine Co. It does not differ from *Oe. ivallda*

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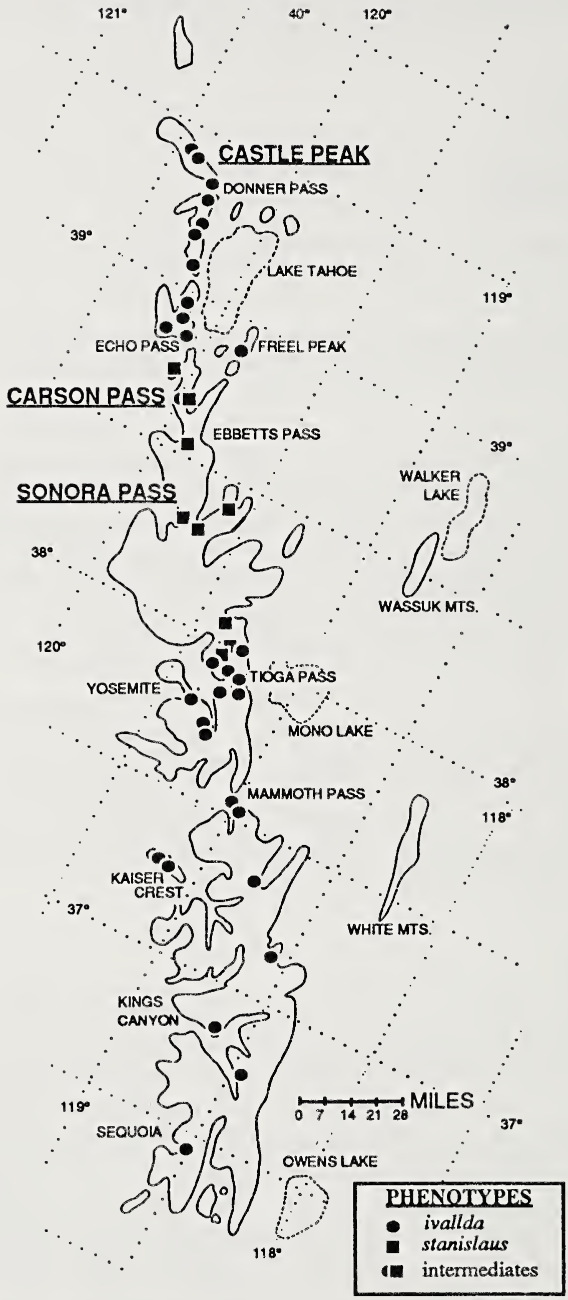

Fig. 1. Distribution of alpine habitats in the Sierra Nevada of California with known localities of *Oeneis ivallda* and *Oe. chryxus stanislaus*, redrawn from Hovanitz (1940) with additional confirmed localities added. Populations sampled in this study are in the larger sized font.

in genital morphology, indeed, the only basis for diagnosis is color, both sexes being a deep "butterscotch" brown. The geographic distribution of *stanislaus* was documented by Hovanitz (1940); it is entirely contained in the central Sierra, from Carson Pass to Tioga Pass, with pure *ivallda* distributed parapatrically to the N and S. His map is updated and reproduced here (Fig. 1). The darkest *stanislaus* occur around Sonora Pass, with a gradual decrease in the frequency of dark phenotypes N-ward to only ~5% at Carson Pass (AMS, unpublished data) and 0% near Donner Pass, but an abrupt transition zone to the S "showing the entire range of variation from darkest to lightest" near Tioga Pass (Hovanitz 1940, p. 371). This appears to be a unique geographical relationship, not reproduced in any pair or set of taxa in the Sierran flora, for example (G. L. Stebbins, *pers. comm.*). Virtually the same phenomenon has been reported in Andean birds, however, under the rubric "leapfrog variation" (Remsen 1984). In the cases discussed by Remsen, the N and S populations are treated as two geographic subspecies, separated by a third, more distinct subspecies.

By 1940 Hovanitz had become convinced *ivallda* and *stanislaus* were in fact conspecific, although authorities subsequent to Hovanitz have differed in their treatments. These authorities based their judgment on inexplicit criteria, without any new biological data to justify them. Garth and Tilden (1963) combined both names under *ivallda* as a single subspecies of the widespread boreal and Rocky Mountain species *chryxus* Doubleday and Hewitson. The same authors treated them as separate species 23 yr later (*Oe. ivallda* and *Oe. chryxus stanislaus*; Garth and Tilden 1986), as did Tilden and Smith (1986) and Miller and Brown (1981). Emmel (1975) also kept them separate, but Scott (1986) recognized both as subspecies of *chryxus*. The difference in wing-pigment chemistry, the only diagnostic character reported to date, is not in itself a basis for recognizing biological species, especially when the color phenotypes intergrade. One way to approach the question of species status independently is to look for biochemical-genetic evidence indicating an interruption of gene flow (discussed below).

The *ivallda*/*stanislaus* problem is interesting from a biogeographic as well as taxonomic standpoint because the localization of *stanislaus* in the central Sierra appears discordant with models of colonization from the N but potentially concordant with immigration from the E, as recognized by Hovanitz (1940):

"It may be postulated (1) That the Sierra Nevada was once entirely populated by a white race and that the brown race has either originated *de novo* in the central part or that it has come in via the high Basin Ranges from other populations of the brown form; (2) that the Sierra Nevada was once populated entirely by a brown race at either end of which genes for whiteness developed greater concentrations, or (3) that a uniform population never did exist in the Sierra Nevada (p. 373)."

Hovanitz notes correctly that all the Rocky Mountain populations of

chryxus are brown, and claims that "Individuals from these populations could more easily reach the Sierra Nevada via the high Basin Ranges which form a series of 'stepping-stones' across the uninhabitable desert areas . . . than any other way."

Because the Sierra Nevada is a young range, with most of the major deformation leading to the modern fault-scarp topography occurring only in the past 3 MY (Bateman and Wahrhaftig 1966) — corresponding with the first evidence of glaciation (Curry 1966) — the origin and evolution of the Sierra Nevada alpine biota represents a relatively recent event. For this reason, it has received the attention of historical biogeographers and community ecologists interested in the evolution of new biotas. The conventional wisdom regarding the origins of the Sierran alpine biota strongly favors a strictly northerly route of colonization of alpine/boreal taxa (such as *Oeneis*) (Sharsmith 1940, Axelrod 1957, 1977; Chabot and Billings 1972), although many endemic plant species evolved *in situ* from dry-adapted continental taxa widespread at lower altitudes (Stebbins and Major 1965).

Scenarios have been promoted involving easterly immigration of some small proportion of the alpine biota from the Rocky Mountains (Harshberger 1911; Major and Bamberg 1967; Major and Taylor 1977), despite objections in the literature (Axelrod 1976). Although the sequence of glacial events and the interglacial vegetation in the Sierra Nevada remains very sketchy (Fullerton 1986), Wells (1983) published data from wood rat (*Neotoma*) middens demonstrating the presence in SE Oregon in full-Wisconsinian glacial time of a prostrate juniper steppe with patterned ground, even below 1500 m. It is not difficult to visualize *Oeneis chryxus* living in such a climate. Wells considers that the low elevation desert trough E of the central Sierra has constituted a major barrier to the W-ward dispersal of Rocky Mt. organisms. The possibility that such organisms came in from the NE (N Great Basin) along the shores of the pluvial lakes, spreading into the Sierra at lower elevations initially on the E flank, must be taken seriously. At least one "easterly" scenario has been borne out: Major and Bamberg's (1967) prediction that *Pinus flexilis* (Pinaceae) would be found to have spread to the Sierra from the E in the Mojave sector has been amply validated by Wells' *Neotoma* data.

The biogeographical and evolutionary-ecological framework for interpretation of the *ivallda/stanislaus* problem differs depending on whether one is dealing with one species or two. As a single species, both forms could have arrived in a polymorphic population colonizing from the N or E; as separate waves of colonists from the same or different directions; or one form could have arisen and spread within the Sierra. The relevant evolutionary questions would involve the biogeography of diagnostic characters alone. This was the type of question addressed by Hovanitz (1940) when he claimed that visual selection for background matching (crypsis) by predators would favor the pale

ivallda morph on granitic substrates and the darker *stanislaus* morph on andesite, and that the geography of the colors matched that of the substrates. If the two forms belong to two species, one might interpret the situation as one of competitive exclusion of *ivallda* by *stanislaus* in the central Sierra; the most interesting questions would address the whole genomes of these taxa from the perspective of community ecology — for example, "What ecological factors limit *stanislaus* to the central part of the high Sierra?" Here, we attempt to test the assumption of conspecificity using electrophoretic characters, in an attempt to refine evolutionary and biogeographical investigations to the proper level of analysis.

Materials & Methods

Three samples were available for this study (Fig. 1): from the ridge between Castle and Basin Peaks, Nevada Co., 2.VII.1989 (*leg.* AMS) (phenotypically pure *ivallda*, no *stanislaus* or intermediates ever recorded in 18 yr) (n = 20); Carson Spur along Hwy. 88, Alpine Co., 4.VII.1989 (*leg.* J. Mori) (mostly *ivallda*, approximately 5% intermediate in long series, occasionally approaching full *stanislaus* in color) (n = 19); and Sonora Pass, Alpine-Tuolumne-Mono Cos., 5.VII.1989 (*leg.* J. Mori) (phenotypically pure *stanislaus*) (n = 19). All individuals were frozen alive at −80°C. The heads and thoraces were homogenized for analysis; all wings and genitalia were retained as vouchers deposited in the Bohart Museum of Entomology at Davis. Every individual was scored as *ivallda*, intermediate, or *stanislaus* independently by both of us; only two individuals (from Carson Spur) were ambiguous (scored as intermediate by one of us, *ivallda* by the other).

Electrophoresis protocol followed Ayala et al. (1972) and Geiger and Shapiro (1986), as modified by Porter and Matoon (1989). 16 loci were studied: adenylate kinase (AK-1; Enzyme Commission number: 2.7.4.7), aldolase (ALDO; 4.1.2.13), glucose-6-phosphate dehydrogenase (G6PD; 1.1.1.49), glutamic-oxaloacetic transaminase (two loci: GOT-1, GOT-2; 2.6.1.1), glyceraldehyde-3-phosphate dehydrogenase (GAPDH; 1.2.1.12), α-glycerophosphate dehydrogenase (α-GPD; 1.1.1.8), hexokinase (HK-1; 2.7.1.1), isocitrate dehydrogenase (IDH-1; 1.1.1.42), malate dehydrogenase (MDH-1, MDH-2; 1.1.1.37), malic enzyme (ME-1, ME-2; 1.1.1.40), phosphoglucose isomerase (PGI; 5.3.1.9), phosphoglucomutase (PGM; 2.7.5.1), and the anodally migrating locus of superoxide dismutase (SOD-2; 1.15.1.1). Zymograms were scored using letter designations, with the fastest allele in the cathodal direction given the letter A. Data were analyzed using the computer program BIOSYS-1 (Swofford and Selander 1981). Formulae for the basic population genetic parameters used here are given and discussed in most introductory population genetics textbooks (e.g., Hedrick 1985) and will not be repeated here. The banding patterns are entirely consistent

Table 1. Allelic frequencies at variable loci.

Locus & allele	Population (*ivallda*) Castle Peak[a]	(*ivallda* + intermediates) Carson Spur[b]	(*stanislaus*) Sonora Pass[c]
AK-1			
A	0.950	0.947	0.947
B	0.050	0.053	0.053
GAPDH			
A	1.000	0.947	1.000
B		0.026	
GOT-1			
A		0.079	0.079
B	0.975	0.842	0.605
C	0.025	0.026	
D		0.053	0.316
α-GPDH			
A	1.000	0.974	1.000
B		0.026	
HK			
A	0.150	0.211	0.071
B	0.850	0.789	0.929
IDH-1			
A	0.100	0.053	0.105
B	0.100	0.105	0.105
C	0.375	0.500	0.553
D	0.425	0.316	0.237
E		0.026	
ME-1			
A		0.026	0.179
B	1.000	0.947	0.821
C		0.026	
PGI			
A	0.375		
B	0.550	0.868	1.000
C	0.075	0.132	
PGM			
A	0.625	0.447	0.263
B	0.375	0.553	0.737

[a] n = 20. [b] n = 19. [c] n = 19, except n = 14 at HK & ME-1.

with those expected from segregating alleles of mono-, di-,and tetrameric enzyme systems reported for these loci in other organisms (Harris and Hopkinson 1976; Kitching 1985). Since no breeding program has been carried out, we made the usual assumptions in treating electromorphs as alleles for the purposes of genetic analysis.

Table 2. Genetic variability in sample populations. A: mean alleles per locus, H_{obs}: observed proportion of heterozygotes, H_{exp}: heterozygote proportions expected from Hardy-Weinberg ratios, P: percent of loci polymorphic, with more than one allele detected. Standard errors in parentheses.

Population	A	P	H_{obs}	H_{exp}
Castle Peak	1.6 (0.2)	37.5	0.128 (0.054)	0.133 (0.058)
Carson Spur	1.9 (0.3)	56.3	0.138 (0.048)	0.146 (0.051)
Sonora Pass	1.6 (0.2)	37.5	0.146 (0.060)	0.132 (0.054)

Results

Allelic frequencies for the nine variable loci are given in Table 1; the remaining loci (ALDO, GOT-2, G6PD, MDH-1, MDH-2, ME-2, and SOD-2) were monomorphic. We found no deviations from Hardy-Weinberg proportions. Genetic variability scores for all populations are shown in Table 2. These values are in the normal range for most invertebrates (Thorpe 1983), including butterflies (AHP, AMS, and HJ Geiger, *unpubl.*), indicating that there is enough genetic variability available to permit differentiation of these populations (and taxa) in the absence of gene flow. Indeed, χ^2 contingency table analyses indicate statistically significant differences in allelic frequencies among populations at four of the nine variable loci (GOT-1: $p < 0.0003$; ME-1: $p < 0.02$; PGI; $p < 0.00001$; PGM; $p < 0.006$). However, analysis using F_{ST} (Wright 1931) indicates that despite statistical significance, this degree of differentiation is biologically minor (GOT-1: $F_{ST} = 0.133$; ME-1: $F_{ST} = 0.083$; PGI: $F_{ST} = 0.212$; PGM: $F_{ST} = 0.088$; other variable loci: $F_{ST} < 0.03$; mean $F_{ST} = 0.081$).

The weak differentiation among populations is perhaps reflected in a more familiar way by the low genetic distances (Fig. 2). Using UPGMA as a clustering algorithm (Sneath and Sokal 1973), eight of ten independent analyses grouped Carson Pass (mostly *ivallda* by wing color) with Sonora Pass (*stanislaus*), white the other two grouped Carson with Castle Peak (*ivallda*). Notably, the distance between nodes in these analyses was small, and the greatest genetic distance shown was always within the range shown by subspecies or consubspecific populations in other animal groups (Thorpe 1983). There was nothing to suggest the interruption of gene exchange expected across a species boundary. Taken together, the genetic analyses indicate that (i) the Carson Pass population is more intermediate than wing color data would suggest, and (ii) these populations are only weakly differentiated.

Discussion

Genetic population structure and species-level taxonomy. — There is nothing in our data which would suggest that the *ivallda* and *stanislaus*

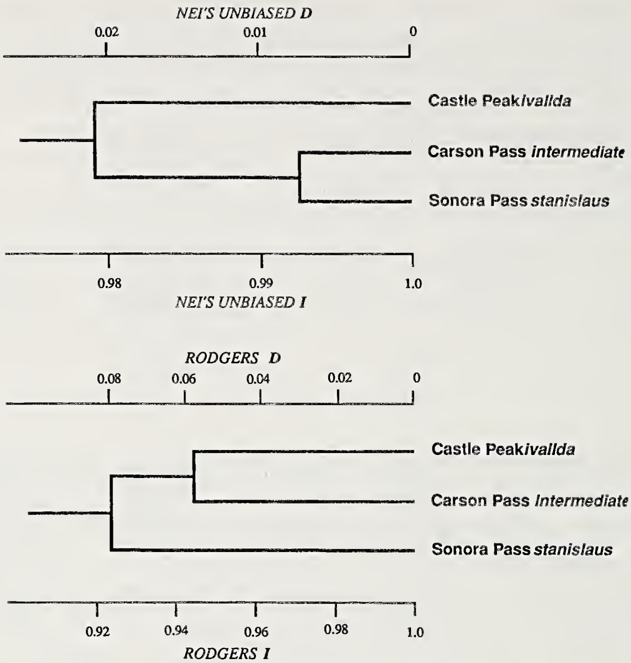

Fig. 2. Genetic distance (Nei 1978, Rodgers 1972) phenograms clustered using UPGMA (Sneath and Sokal 1973). The distances shown are well within the ranges exhibited by subspecies in most butterflies studied. Their lack of concordance indicates the close relationship between these populations.

populations belong to separate species. We found intermediate wing color phenotypes, no diagnostic enzyme loci, and no consistent clinal patterns from locus to locus. At the same time, it must be stressed that analyses of electrophoretic data are logically designed to detect interruption of gene flow. Failure to detect such interruption is not equivalent to demonstrating that gene flow is occurring, because very similar allelic distributions could conceivably be generated by parallel stabilizing selection even in the absence of gene exchange. However, alternative scenarios which do not invoke gene flow become less probable as more loci are examined and found with high similarities: each enzyme locus is likely to respond differently to selection pressures (Carter and Watt 1988), but all loci respond similarly to gene flow.

By assuming that selection on enzyme alleles is weak when averaged over loci, and with the knowledge that genetic drift inescapably differentiates populations, we can use population genetic theory to generate a simplest-case scenario to explain the observed genetic similarity in terms of gene flow. This scenario represents a most-parsimonious hypothesis which can potentially be falsified with data from additional

enzyme loci, with knowledge of the responses to selection by the alleles at sampled loci, or with evidence of geographic variation in previously undetected alleles. If the gene flow estimate we generate is high, then the populations are conspecific under the most parsimonious interpretation of the data.

Under an infinite island model with no selection, the F_{ST} scores we report are explainable by genetic drift counteracted by an average gene exchange rate of approximately 2.8 individuals migrating between these populations each generation (using Wright's [1931] formulation $Nm \approx (1/F_{ST} - 1)/4$, where Nm is the rate of gene exchange among populations). This gene flow rate is sufficiently strong to unite the gene pools of these populations (Wright 1931). However, the infinite island model of population structure seems unrealistic for *Oeneis*. We have observed "hilltopping" behavior (Shields 1967) in both *ivallda* and *stanislaus*: males aggregate on mountain peaks and ridges in search of receptive females. This mating system and the relative continuity of the alpine habitat (Fig. 1) imply that these butterflies are distributed among geographically adjacent or semi-connected populations, and are better described using an isolation-by-distance model of population structure. When sampled populations are separated by intervening populations in an isolation-by-distance model (as here), then the gene flow estimated from F_{ST} represents the average rate of genes diffusing between the sampled populations — the rate of individual animals actually exchanged is a function of the distance between samples, and can be much higher between adjacent local populations (Slatkin and Barton, 1989). Thus, under a model of genetic population structure which seems realistic for these butterflies, gene flow between these taxa is likely to be only weakly interrupted at best.

Although *Oeneis* seem ideal for mark-recapture experiments, no estimates of individual dispersal are presently available to compare against our estimates from genetic data. Garth and Tilden (1963, p. 77) document the ability of *ivallda* to colonize an unusual habitat 300 m lower in elevation than others. AMS visits Donner Pass (2100 m), 2 km from Castle-Basin Peak, regularly during *Oeneis* flight season and has observed two individual *ivallda* there in 18 yr (1 male, 1 female), a high enough incidence to suggest fairly frequent dispersal beyond the alpine zone. The distribution of *Oeneis* in W Nevada (discussed below) also suggests the ability to move among habitat patches.

Taxonomists often assume that characters diagnostic of parapatric or allopatric taxa are indicative of more fundamental genetic differentiation. If Hovanitz's (1940) scenario is correct, the two *Oeneis* color morphs are maintained by selection for crypsis on different substrates. Such a selection differential will erect a partial barrier to the flow of genes between them (Barton 1979, 1983). The barrier and its resulting cline arise because neutral genes are linked on the chromosomes to the color genes experiencing selection, and can only cross the barrier

after recombination links them to the favored color alleles. The presence of this barrier might seem to indicate that the genetic similarity shown between these taxa is an artifact of history rather than a result of contemporary population processes. However, Barton and Bengtsson (1986; see also Barton 1986) have shown that such a barrier will only slow neutral genes, but cannot stop them for long unless (a) there is very strong selection against intermediate genotypes *and* (b) there are so many genes involved in the characters under selection that recombination will not provide an escape from linked deleterious alleles. Thus, current theory supports the notion that the diagnostic character (color) distinguishing *ivallda* from *stanislaus* should be treated as genetically independent of other potential taxonomic characters — an unreliable indicator in itself of species status or gene flow. A similar lack of congruence between wing characters and electrophoretic data has been found by Porter and Geiger (1988) and Porter and Mattoon (1989) in the Satyrine genus *Coenonympha*. There is no biological inconsistency between the distribution of wing color morphs and our electrophoretic data.

The taxonomy most consistent with the available data recognizes *ivallda* and *stanislaus* as members of the same biological species. The genetic relationship between these taxa and the polytypic *Oeneis chryxus* remains unclear, but we recommend that *ivallda* and *stanislaus* remain classified as subspecies of *Oe. chryxus* pending further study. In the meantime, the evolutionary interpretation of the *ivallda/stanislaus* distribution problem is best addressed from a population biology, rather than community ecology, perspective – that is, the evolutionary ecology and biogeography of individual *ivallda* and *stanislaus* traits should be considered separately.

How convincing is the crypsis scenario? — In the S, which Hovanitz knew best, the geography of substrate color matches *Oeneis* color morph distributions quite well. Slemmons (1966, p. 206) maps the central Sierran andesites; the S limit of the andesite belt is in fact at Tioga Pass, and to the S the alpine is nearly pure granite with some darker volcanic rock in the vicinity of Mammoth Mt. The zone of rapid transition from *stanislaus* to *ivallda* morphs in the S corresponds well to this conspicuous feature of Sierran geology, although detailed mapping of color frequencies remains to be done.

In the N, the alpine zone is more fragmented, and probably not all *Oeneis* populations are known. Most of the northern alpine is, however, on andesite — not granite. There is no corresponding geological feature to account for the reappearance of the *ivallda* morph and the gradual N-ward disappearance of the dark *stanislaus* phenotype. At Carson Pass some 75% of the *Oeneis* habitat is on andesitic mudflows (lahars) of the same character and color as those illustrated by Hovanitz, but the frequency of the *ivallda* morph is high (95%). The rarity of dark and intermediate morphs there strongly suggests that something other than background matching is limiting their N-ward spread: a selection

regime strong enough to produce the sharp cline at Tioga Pass should also favor the *stanislaus* morph at Carson. (It remains possible that the hypothetical predator drops out or switches prey just S of Carson Pass.) There is granitic alpine in the Crystal Range WSW of Lake Tahoe — although it is unlikely that the high frequency of the *ivallda* color morph at Carson Pass could be maintained by massive gene flow from there, this may be the historical source of the three N-most *ivallda* populations (Mt. Lola, Castle-Basin Peaks, Anderson Peak). However, given the inconsistencies in the crypsis scenario for *ivallda* populations in the N (Hovanitz [1940] discussed the tenuousness of crypsis and mimicry hypotheses when experimental data were unavailable), we recommend that it be treated cautiously pending experimental confirmation with a known predator.

Plausibility of an Easterly Invasion by the stanislaus Color Genes — Austin and Murphy (1987) recorded the *ivallda* morph in Nevada only in the Carson Range (Carson City and Washoe Cos.), just a few km E of the Sierra Nevada, and nominate Rocky Mountain univoltine *chryxus* in extreme E Nevada (Elko, Lincoln, White Pine Cos.). Since then *stanislaus* (indistinguishable from Sierran) has been found in the Sweetwater Mts. in Lyon Co. on the California border, again just a few km E of that morph's range in the Sierra Nevada (G. T. Austin, *pers. comm.*). These occurrences seem to be due to W-to-E dispersal from the Sierra, and are uninformative about colonization routes into the Sierra. An absence of relictual *Oeneis* in central Nevada is mirrored in other alpine butterflies, and in other alpine organisms generally (Billings 1978, Harper and Reveal 1978).

The genetic analyses provide no additional characters associated with either *ivallda* or *stanislaus* morphs for comparison to other *chryxus* populations to the N and E, leaving wing color as the only reliable character. All other *chryxus*, and most other *Oeneis*, are colored like *stanislaus*, or even darker (Ferris and Brown 1980). In the absence of a phylogeny for *Oeneis*, we assume that the original invaders of the Sierra were this color and that the *ivallda* color is a uniquely derived autapomorphy. But if the *stanislaus* morph came from the N, why are the relict plesiomorphous color genes in the central Sierra and not also in the N — especially if andesitic substrates are relevant? As Hovanitz noted, the distribution would make more sense if the invasion of the *stanislaus* color genes had come directly across the Great Basin. *Oeneis chryxus* apparently does not occur in Oregon (Dornfeld 1980) or in the Klamath Mts. of N California (Shapiro et al. 1981), reaching its southern limit (W of the Rockies) in Washington. Its range as mapped by Scott (1986, p. 248) raises a very serious question of where an invasion from the N might have come from; no relicts of the hypothetical N route have been found.

At least one other butterfly taxon is distributed along the hypothetical NE invasion route. *Limenitis lorquini weidemeyerii* (Edwards), a Rocky Mountain middle-elevation nymphalid butterfly, is restricted to

montane riparian canyon habitats in the Great Basin (Austin and Murphy 1987; Porter 1989). Its distribution closely follows the colonization route in the Humboldt drainage proposed by Major and Bamberg (1967): it crosses the low-elevation desert into the Wassuk Mts. and reaches its W distribution limits on the N shore of Mono Lake (see Fig. 1), where it hybridizes with the Sierran *L. lorquini lorquini* (Boisduval) (Porter 1989). "Pure" *L. l. weidemeyerii* and hybrid wing pattern morphs are sympatric with *Oe. c. stanislaus* near Sonora Pass where montane and subalpine habitats interdigitate. The distribution of the *weidemeyerii* morph is entirely consistent with an invasion of *stanislaus* color genes from the E into the central Sierra. The presence of *L. lorquini burrisoni* Maynard (a weakly defined taxon quite similar in phenotype to nominate *lorquini*) in Oregon, Washington and into western Montana makes a northerly route of Sierran invasion by the *weidemeyerii* form seem highly unlikely. Although *Limenitis* is found in montane habitats and *Oeneis* rarely strays from the alpine, similar immigration corridors may have been used at different times by both.

The simplest scenario consistent with the *Oeneis* distribution data has *chryxus* invading first (from the N or E) and evolving the distinctive *ivallda* color, with a second *chryxus* invasion from the E injecting the distinctive *stanislaus* color into the central Sierran populations. However, this is by no means the only available scenario, and it is even possible that the butterscotch brown of the *stanislaus* morph represents a character reversal, and not evidence of two Sierran invasions. Genetic studies of the entire *Oeneis chryxus* complex in western North America, with an eye towards alleles linking Sierran and potential source populations, may expose characters which will help resolve the biogeographical problem. The answer will be of considerable value in the interpretation of the origins of the entire Sierran alpine biotic community.

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A New *Polythrix* From Central America (Lepidoptera: Hesperiidae)

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Abstract. *Polythrix kanshul* is described as a new species. It differs from its nearest relative, *P. metallescens* in several details of wing pattern and in many genitalic characters. These two species, along with *P. eudoxus*, form a monophyletic lineage defined by the morphology of the uncus. *Polythrix kanshul* in known from Palenque, Chiapas, Mexico and Bayano, Panama.

The genus *Polythrix* is distributed from the southern border of the United States south to Argentina with the bulk of the 15 recognized species found in Central America and northern South America (Evans 1952). Freeman (1979) recorded six species in Mexico and provided a key to their identification while Llorente, et al, (1990) listed seven species. While identifying material from southern Mexico, I realized that a new species of *Polythrix* was present in the sample. My purpose here is to describe it and to document its relationship with other species in the genus.

Polythrix kanshul, Shuey New species

Diagnosis of male: The wing pattern (Figures 1-4) of *P. kanshul* is very similar to *P. metallescens* (Mabille) (Figures 5-8) with the following exceptions: the ground color of *P. kanshul* is darker brown and the dorsal metallic blue-green body and hindwing scaling is brighter than in *P. metallescens*; *P. kanshul* has four apical spots, *P. metallescens* has three; and ventrally, the narrow white discal band on the hindwing is shorter in *P. kanshul*, extending only between veins 2A and Cu_2 while in *P. metallescens* this band extends between veins 2A and $Sc+R_1$. A color photograph of *P. metallescens* can be found in Lewis (1973).

Description of male: Figures 1-4. Forewing: ground color brown; fringes brown; metallic green hairs cover the basal one-third dorsally — one-sixth ventrally; four apical spots present; three hyaline spots - one located in the distal portion of the discal cell and one each in the mid-points of cells M3 and Cu_1; costal fold present; ventral hair-tuft covers the origin of vein Cu_2; ventral cells Cu_2 and 2A gray. Hindwing: ground color brown; fringes white; vein 2A extended, forming a blunt tail; metallic green hairs and scales cover the inner two-thirds dorsally — one-third ventrally extending downward at the tails; ventral surfaces with a narrow white discal band between veins 2A and Cu_2. Head, palpi, and

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Figures 1-4. *Polythrix kanshul*; 1, dorsal view, holotype male, Palenque, Mexico; 2, ventral view of previous specimen; 3, paratype male, Bayano, Panama; 4, ventral view of previous specimen.

Figures 5-8. *Polythrix metallescens*; 5, dorsal view; male, Madden Forest, Panama, 3 Aug. 1969; 6, ventral view of previous specimen; 7, female, Cayuga, Guatemala, May; 8, ventral view of previous specimen.

thorax ground color brown but densely covered with metallic green hairs and scales.

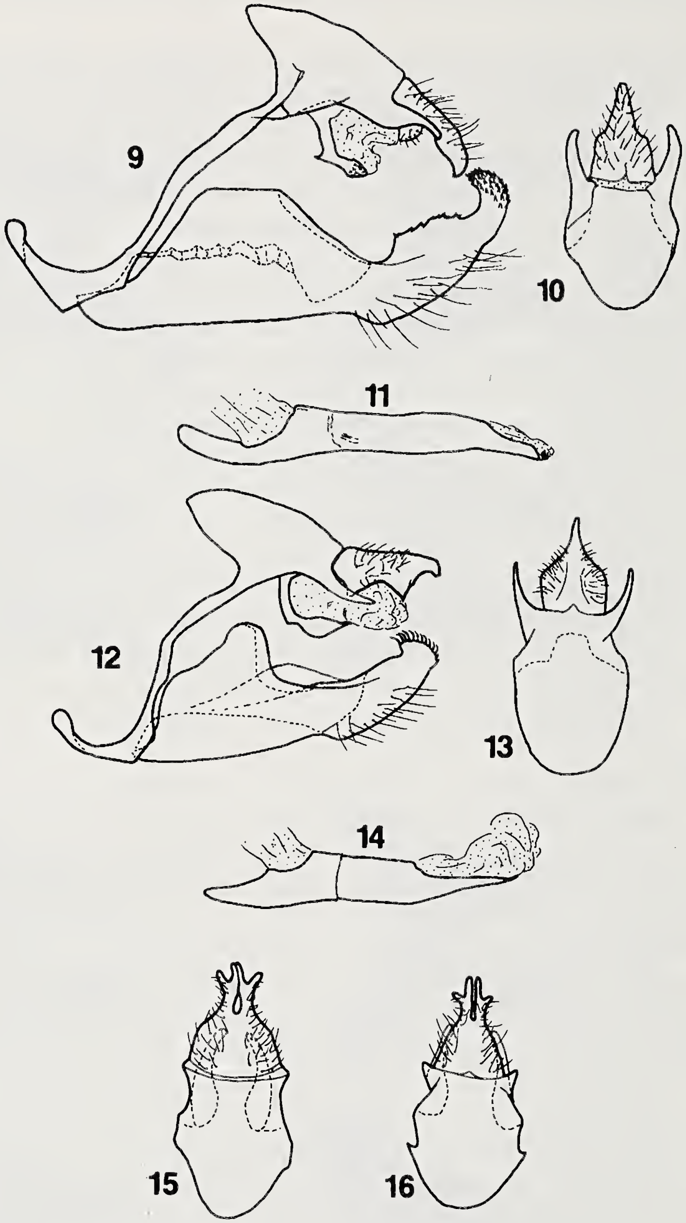
Male (Figure 9) valvae elongated into a curved, heavily toothed, blunt projection; upper edge of sacculus (sensu Klots, 1970) heavily sclerotized and wrinkled. Uncus (Figures 9-10) fused into a single posterior projection with lateral socii originating from tegumen on both sides. Aedeagus (Figure 11) with anterior extension beyond membranous ejaculatory duct; posterior cornuti plate-like and hinged ventrally.

Female: Unknown. If the pattern of sexual dimorphism is similar to that of *P. metallescens* (Figures 7-8), the female of *P. kanshul* should be similar to the male, but with longer tails and duller green iridescence.

Types: Holotype - Mexico, Chiapas, Ruinas Palenque, approx 17°30' X 92°05', 21-VIII-1987, J.A. Shuey, collector (Carnegie Museum of Natural History). Paratypes - one specimen with the same locality data as the holotype, collected 20-VIII-1987 (J. A. Shuey collection): One specimen, Panama, Panama, Bayano, 12-X-1974, G.B. Small, collector (United States National Museum of Natural History).

Etymology: The specific name reflects the long and splendid history of the type locality, Palenque, and is a latinization of Kan-Xul (kan-shóol). Kan-Xul was the second son of Pacal to assume the rulership of Palenque, and along with his father and brother, was responsible for much of the magnificent architecture of this site. Kan-Xul ruled Palenque at its zenith, but was captured in warfare with neighboring Tonina, and presumably sacrificed there (Schele and Miller, 1986). An accession portrait of Kan-Xul, in stucco relief, still survives within the palace at Palenque. Kan xul is Mayan for "magnificent animal". My name for this insect is meant as a double tribute; first to the Maya, past and present, whose world view and beliefs continue to shape much of Central America; second, to the insect, which is truly 'kan xul'.

Habitat and Distribution: The habitat at Palenque is mature to young "selva alta perennifolia" (perennial high rainforest) (Miranda and Gyves, 1979). The entire forest in the vicinity of the ruins has presumably regrown since approximately 1000 BP. The classic Maya developed the entire area around the core of the ruins, and little or no forest probably occurred in the immediate vicinity at the time of active occupation (Andrews, 1975). Portions of the present day forest represent the original old-growth forest that blanketed the site after Palenque was abandoned, but much of the surrounding forest represents more recent regrowth that followed the clearing of the ruins during the late 1800's to the present. The holotype was captured along a well worn trail through a part of the rainforest that may represent part of the older growth. It was perched on the underside of a leaf when captured. The other Palenque specimen was collected at a nearby motel which is surrounded by young rainforest regrowth. This specimen was collected at night on a white sheet illuminated by ultraviolet light. It was probably dislodged from its



Figures 9 - 11. *Polythrix kanshul*, holotype male genitalia; 9, lateral view; 10, dorsal view of uncus and tegumen; 11, lateral view of aedeagus.

Figures 12 - 14. *Polythrix metallescens*, male genitalia; 12, lateral view; 13, dorsal view of uncus and tegumen; 14, lateral view of aedeagus.

Figures 15 - 16. *Polythrix genitalia*, uncus and tegumen, dorsal view; 15, *P. caunus*, R. Yanacani, E. Bolivia, alt. 600m., March 1915; 16, *P. auginus*, Cayuga, Guatemala, August.

nocturnal perch during an intense evening rainstorm, and subsequently attracted to the light.

The perennial high rainforest habitat is widespread throughout the lowlands of Central America, and *P. kanshul* is probably found in all of the intervening countries between Chiapas and Panama. Perennial high rainforest in Mexico extends northward into Tabasco and in fragmented form into Veracruz, and of course, southward throughout much of South America; *P. kanshul* should occupy a more extensive area than is presently known. Like all rainforest life, this species is certainly extirpated from the portions of its original range which have been converted for agricultural uses.

Discussion: *Polythrix kanshul* and *P. metallescens* are each other's closest known relatives. They differ from all other *Polythrix* species in the distinctive configuration of the hyaline forewing spots and in the relatively large amount of metallic over-scaling on the wings and body. In other species of *Polythrix*, the forewing spots are fairly broad and overlap. These overlapping spots, in conjunction with the prominent apical spots and hindwing tails, give the genus *Polythrix* its distinctive appearance. In *P. kanshul* and *P. metallescens* these spots are taller than they are wide, and generally do not overlap.

Despite their similarities, I would argue that the divergence of *P. kanshul* and *P. metallescens* from a common ancestor is not recent. While the genitalia of these two species differ most conspicuously in the configuration of the valvae, the details of almost every other structure differ also (Figures 9 - 14). The accumulation of so many structural differences indicates that these taxa have followed different evolutionary paths for a long time. The broad geographic overlap of these two taxa also supports this contention. *Polythrix metallescens* occurs from Belize south through Central America and into at least amazonian Brazil. *Polythrix kanshul* is known from Panama and Chiapas Mexico, indicating a broad overlap in the known range of these two species. Recent differentiates are generally allopatric.

The fused uncus is apparently an apomorphy which defines a lineage composed of three species, *P. metallescens*, *P. kanshul*, and *P. eudoxus* (Stoll). My inclusion of *P. eudoxus* in this lineage is somewhat tentative, but Evans' (1952) caricature of the genitalia of this species suggests that it too has the fused uncus and lateral socii. All other species of *Polythrix* have a more typical Pyrginae uncus composed of two lateral prongs. However, some of these species may form a transition series to this apomorphic character state; *P. caunus* (Herrich-Schäffer) and *P. auginus* (Hewitson) for example, have the basal portion of the uncus elongated, with the two prongs reduced to small hooks on the distal end (Figures 15 and 16), and the beginnings of enlarged lateral socii. The homology of this transitional state is tentative, but its configuration is certainly suggestive.

The addition of *P. kanshul* to Mexico's fauna raises the number of

Polythrix species known from that country to eight. It seems likely that *P. metallescens* also will be found to occur in southern Mexico. This skipper is known from Belize and Guatemala, and may eventually be found in the dense rainforests of the Lacadón Forest and Montes Azulies Biosphere Reserve of eastern Chiapas.

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Three unusual species of *Paracles* from South America (Lepidoptera: Arctiidae)

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Abstract. Two new species of *Paracles* Walker are described from the northern Andes, which differ from congeners by their small size and uniform brown coloration: *Paracles minuta* n. sp. (Colombia) and *P. diminuta* n. sp. (Venezuela). *Thagona medinata* (Dognin) is recognized as a *Paracles*, and transferred from Lymantriidae; it differs from other *Paracles* in its immaculate white coloration.

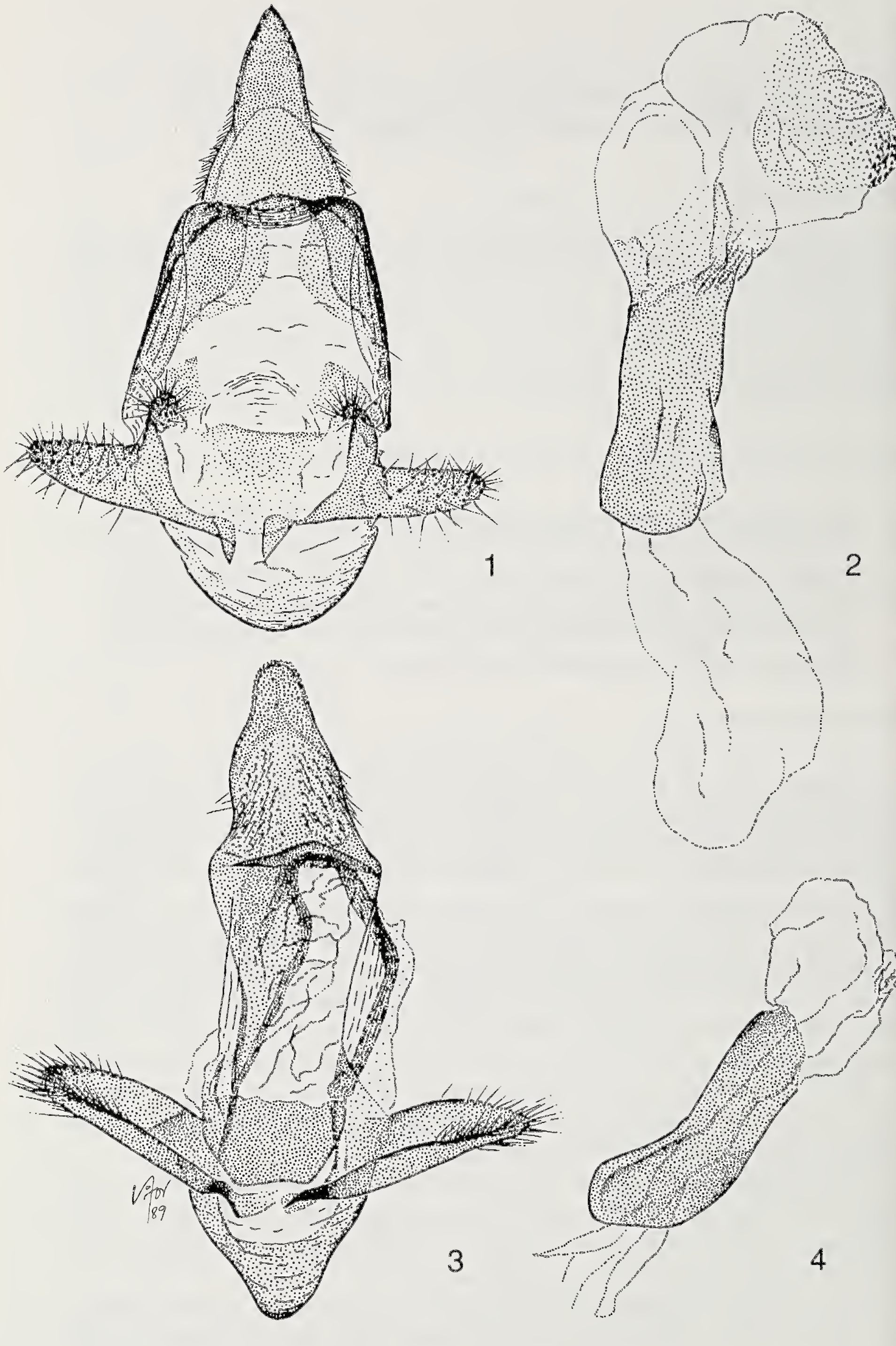
Introduction

In the course of research on zygaenoid moths, we encountered two undescribed species of the arctiid genus *Paracles* Walker which superficially resemble megalopygids, especially *Podalia bolivari* (Heylaerts) (Miller and Becker, in press). These two species are very similar to the few uniform brown species of *Paracles*, especially *P. obscurior* (Schaus) (see Watson, 1973: 33, pls. 31d, 89a, b), but differ from these in their much smaller size (forewing lengths of about 9 mm versus 18 mm). Both the new species are known only from males. It is possible that the females are brachypterous, as are some others in the genus, e.g., *Paracles deserticola* (Berg, 1875: 212) and *P. imitatrix* (Rothschild, 1922: 493).

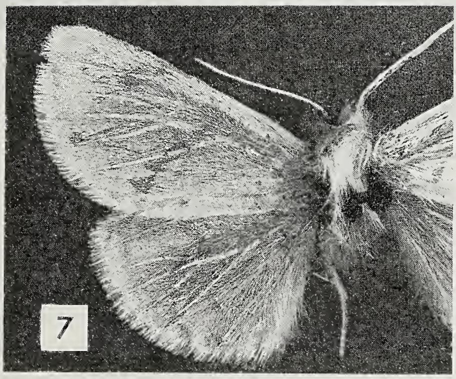
We also take the opportunity to transfer *Thagona medinata* (Dognin) from the Lymantriidae to its proper place among *Paracles*, and give illustrations to permit its identification.

The proper generic name of this group has been confused in the past. We follow Watson (1980) and Watson and Goodger (1986: 32) in using *Paracles*. Before Watson and Goodger (1986), most of the species were placed in *Palustra*, *Antarctia*, or *Maenas*.

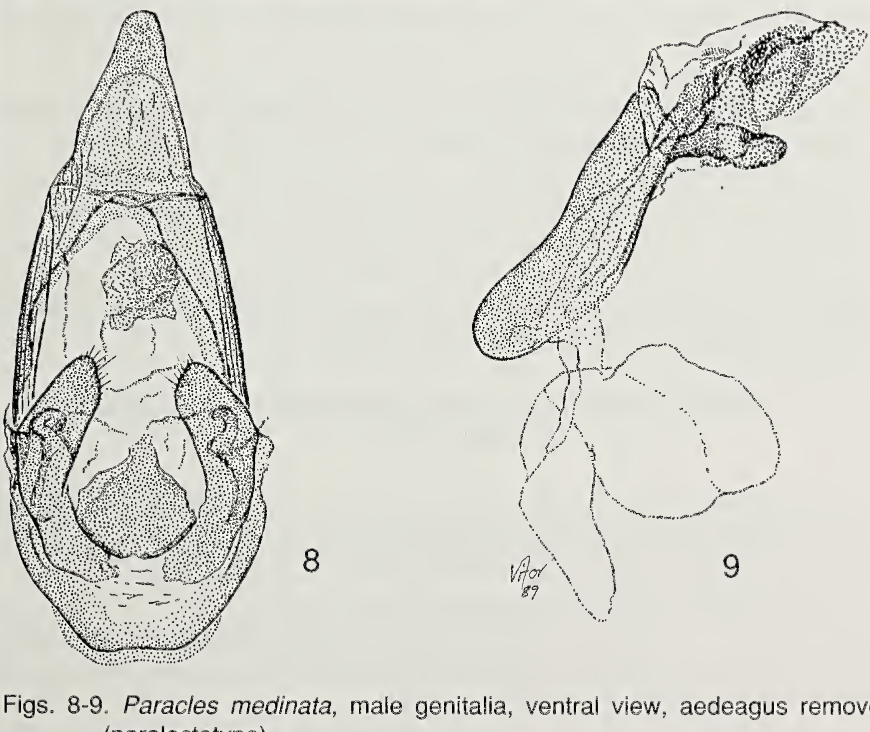
Holotypes are deposited in the National Museum of Natural History (USNM). Other collection acronyms follow Heppner and Lamas (1982).



Figs. 1-4. *Paracles* male genitalia, ventral view, aedeagus removed (paratypes); Figs. 1-2: *P. diminuta*; Figs. 3-4: *P. minuta*.



Figs. 5-7. *Paracles* male left wings; Fig. 5: *P. minuta* (holotype); Fig. 6: *P. diminuta* (holotype); Fig. 7 *P. medinata* (lectotype).



Figs. 8-9. *Paracles medinata*, male genitalia, ventral view, aedeagus removed (paralectotype).

Taxonomy

Paracles minuta Becker & Miller, new species
Figs. 3-5

DIAGNOSIS.-Very similar to *Paracles obscurior*, but much smaller and with darker ground color. Similar to *P. diminuta*, but antennae with longer ciliation and forewings lacking maculation at end of discal cell (Fig. 5); base of valva lacking setose costal lobe (Fig. 3).

ADULT MALE (Fig. 5).-Forewing length 8.5 mm.

Head densely hairy, dark brown. Antennae strongly bipectinate, pectinations three flagellum diameters long. Thorax and abdomen densely hairy, dark brown dorsally, pale brown ventrally. Legs pale brown, tarsi with light and dark brown banding. Forewings dark brown, costal margin slightly concave, thinly scaled with elongate scales yielding translucent appearance. Hindwings similar, slightly lighter. Ventral wings lighter, except costal margins which are dark brown with some patches of lighter scales.

MALE GENITALIA (Figs. 3, 4).-Uncus tapered, slightly expanded at middle, apex rounded; tegumen long, bent ventrad; valvae short, simple, covered with short setae distally; juxta an inverted, broad trapezium; saccus triangular, slightly rounded anteriorly. Aedeagus short, bent ventrad at middle; vesica smooth (one of two preparations has a very long, thin cornutus; presumably lost in preparation of the second specimen).

ADULT FEMALE.-Unknown.

TYPE LOCALITY.-Colombia, Cundinamarca, Bogotá, "Pueblo Guasca".

IMMATURE STAGES.-Unknown.

FLIGHT PERIOD.-Unknown.

DISTRIBUTION.-Known only from the vicinity of Bogotá, Colombia.

MATERIAL EXAMINED.-Holotype (USNM) and 33 male paratypes: COLOMBIA: *Cundinamarca*: Bogotá, 2800-3200 m [no date], A.H. Fassl (USNM); "Pueblo Guasca, Bogotá", [no date], "F. Johnson/donor" (BMNH, BPBM, CMNH, LACM, USNM, VOB, ZSBS).

Paracles diminuta Becker & Miller, new species
Figs. 1, 2, 6

DIAGNOSIS.-Similar to *Paracles minuta*, but forewings more rounded and with pale mark across end of discal cell (Fig. 6), and antennae with shorter ciliation; base of valva with setose costal lobe (Fig. 1).

ADULT MALE (Fig. 6).-Forewing length 9 mm.

Entirely brown, except vertical tan line at end of discal cell. Hindwing slightly lighter than forewing. Antennae narrow, without pectination; ciliation as long as flagellum diameter.

MALE GENITALIA (Figs. 1, 2).-Uncus tapered, slightly constricted at

middle; apex pointed; tegumen rounded; valvae simple, narrow, base of costa expanded into a short, irregular lobe covered with short setae; juxta weak, nearly rectangular, slightly constricted laterally; saccus broadly rounded. Aedeagus nearly straight; vesica expanded, with a broad scobinate area; a small area with short, triangular spines at edge of scobinate area.

ADULT FEMALE.-Unknown.

TYPE LOCALITY.-Venezuela, Meridá, Mucuy Fish Hatchery, 7 km E of Tabay, 6600 feet [2000 m].

IMMATURE STAGES.-Unknown.

FLIGHT PERIOD.-February.

DISTRIBUTION.-Known only from the type locality.

MATERIAL EXAMINED.-10 males from the type locality (holotype [USNM] and 9 paratypes), all collected 10-13-II-1978 by J.B. Heppner at blacklight (BMNH, LACM, UCV, USNM, VOB).

Paracles medinata (Dognin), new combination
Figs. 7-9

?Trochuda medinata Dognin, 1920: 4.
Thagona medinata: Schaus, 1927: 549, pl. 74c.

This species was described from an unspecified number of males and one female from "Medina, est de la Colombie, 500 metres (Fassl)". Three males and one female from the Dognin Collection are present in the USNM; we hereby designate the male which bears Dognin's "type" label, as well as USNM type number 29743, as lectotype. We hereby transfer this species to Arctiidae. The characters of wing venation, antennae, and male genitalia are typical of *Paracles*, and very similar to others in the genus (as illustrated by Watson, 1971, 1973).

A series of specimens has been collected at Planaltina, DF, Brazil, by the first author.

Acknowledgements. Most of this work was carried out at the Smithsonian Institution. The photographs were taken by Victor Krantz of the Smithsonian Institution. D.C. Ferguson, Systematic Entomology Laboratory, U.S. Department of Agriculture, assisted in placing the new species. J.P. Donahue, D.C. Ferguson, and J.E. Rawlins reviewed the manuscript.

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Selection of Lepidopterologically Interesting Areas in Central Spain Using UTM Distribution Maps

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Abstract. This paper deals with species richness and biogeographic interest of the butterfly fauna (*Papilionoidea* & *Hesperioidea*) of the Madrid province, using its one hundred and nine 100 sq. km UTM squares data. Richest species squares (80-102 species) are on the north (Sierra de Guadarrama) and the poorest ones on the centre and south. There is a slightly rich area on the southeast. Fauna's biogeographic interest (chorological index *sensu* Kudrna) shows a different pattern, being maximum on the southeast squares, lightly high on the south and centre, and low on the north. In conclusion, richest species squares are not necessarily those of maximum average chorological index. This is explained by the environmental similarity (climate, vegetation, etc) between Sierra and the European generality , while plant formations on the south (typically xerophytic) are peculiar in comparison with the rest of the continent, which have been used as a biogeographic reference. Consequently, species richness appears as a limited criterion when focussing the selection of areas lepidopterologically interesting. Qualitative criteria must be also considered to establish possible zones to protect their butterfly communities, such as the biogeographic interest of the fauna, provided by UTM species distribution maps.

Resumen. Este trabajo estudia el número de especies y el valor biogeográfico de la fauna de mariposas (*Papilionoidea* & *Hesperioidea*) presente en cada una de las 109 cuadrículas UTM de 100 kilómetros cuadrados de la provincia de Madrid. Las cuadrículas con mayor número de especies (entre 80 y 102) se sitúan al norte del territorio (Sierra de Guadarrama) y las más pobres en el centro y sur. Al sureste hay una zona moderadamente rica. El valor biogeográfico de la fauna (índice corológico de Kudrna) tiene un reparto bien distinto, ya que es máximo en las cuadrículas del sureste, moderadamente alto en el sur y centro, y bajo en el norte. Se infiere, por tanto, que las cuadrículas más ricas en especies no son necesariamente las de mayor índice corológico medio, lo que atribuimos a la similitud ambiental (clima, vegetación, etc) de la Sierra con la mayor parte de Europa, mientras que las formaciones vegetales del sur (encinares, coscojares y quejigares sobre todo) son más singulares (más xerófilas) con respecto al continente, ámbito de referencia biogeográfica utilizado. Concluimos con que el criterio del número de especies es de utilidad limitada en la selección de áreas de interés lepidopterológico, y que son necesarios también criterios cualitativos, como el valor biogeográfico de la fauna, para establecer zonas susceptibles de protección por su fauna de mariposas, a partir de mapas UTM de distribución de las especies.

Introduction

Decreasing numbers in many butterfly and skipper populations are awakening, among numerous naturalists, the interest for their conservation.

Obviously , the bigger the information about species the more efficient will be the measures to propose towards its conservation. Therefore, it is necessary to deep in the knowledge of some aspects such as the precise geographic distribution, environmental preferences, life cycles, interactions with foodplants, parasites and any other biological aspect affecting different species. But, in view of the fast butterfly and skipper communities impoverishment process, generally caused by different human activities, it is fairly evident that we can not wait the results of the aforementioned autoecological studies to adopt protection criteria.

Nevertheless, we believe suitable to begin applying protection measures based only on geographic range data, given that, as repeatedly has been said, ecosystem conservation, as opposed to species approach to butterfly protection, would seem to be the most effective policy to be followed (Thomas & Mallorie, 1985; Munguira, 1987; Viejo, Viedma & Martinez, 1989). And Lepidoptera atlases are very useful for those preliminary studies.

In some European countries, such as Great Britain (Heath & Skelton, 1983) or Switzerland (Gonseth, 1987), their butterfly distribution maps are already concluded, at a national scale and following UTM 100 km^2 squares system. On the opposite, in Spain we are still well behind to complete our butterfly distribution national maps, although a valuable effort on the elaboration of regional atlases within the last ten years has been made, and some of them, both from the north (Gomez de Aizpurua, 1977; 1979; 1988) as well as from central Spain (Viejo, 1983; Gomez de Aizpurua, 1987) have been already published.

Methods

The Atlas of the Lepidoptera of Madrid (Gomez de Aizpurua, 1987) provided data for this study, which compiles 153 distribution maps of species of *Zygaenoidea*, *Papilionoidea* & *Hesperioidea* in the Madrid province. We have excluded the 13 species of *Zygaenoidea*, and from the lasting 140 we have eliminated 4 because of uncertain data, as well as the records prior to 1950 with no later confirmation.

A presence-absence matrix (1-0) with the faunistic data from the one hundred and nine 100 km^2 squares of Madrid was made.From this matrix we could obtain the species number and the Average Chorological Index (Kudrna, 1986) of each square, which have been used as criteria to establish the conservation interest of the study area, given the linking relationship between butterflies and specific vegetation communities (Uherkovich, 1983; Viejo & Templado, 1986).

Species number is a variable frequently used in conservation studies (Margules & Usher 1981; Galiano, Sterling & Viejo, 1985; Usher,1986), because of its convenient obtention and handling, although it offers, by itself, just a limited information.

The chorological index proposed by Kudrna (*op. cit.*)is used here, having been

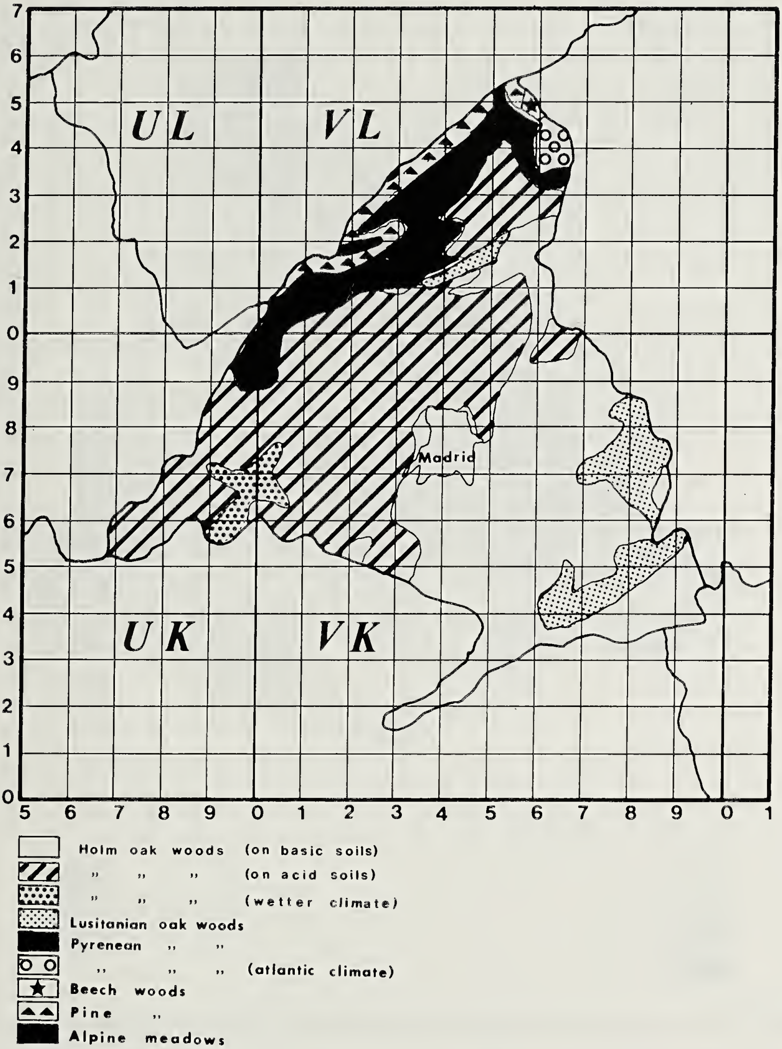

Fig. 1. Map of the climax vegetation of Madrid province (modified from Rivas Martinez, 1982).

used before by the authors in butterfly conservation studies (Sanchez & Viejo, 1988; Viejo & Viedma, 1988; Viejo, Viedma & Martinez, *op. cit.*) and it is the sum of three variables related to species range: size, composition and affinity. This index ranges from 4 to 14; high values mean biogeographically peculiar species (European endemic species with a very small range), while low values correspond to widely distributed species. The mean of the chorological index of the species occuring within a square is the square's Average Chorological Index. The higher this value, the more peculiar fauna, biogeographically speaking, in the considered square.

Data were processed with the BMDP 1D program at the Computer Center of the Universidad Autónoma de Madrid.

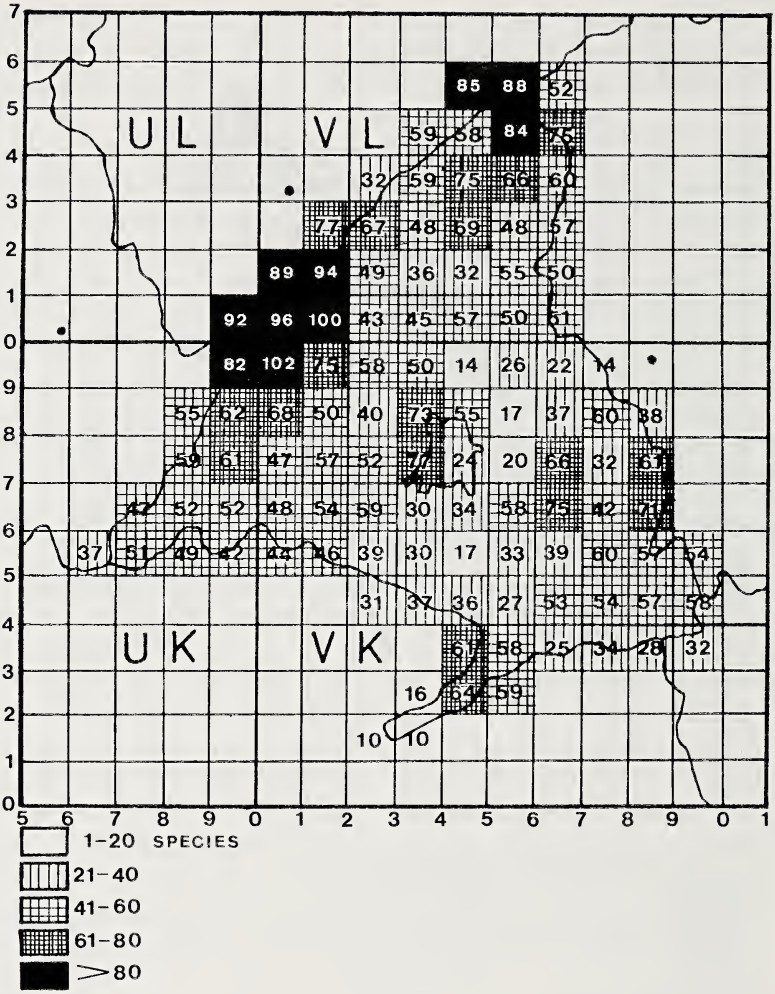

Fig. 2. Map of species richness in each 100 km² UTM grid in Madrid province.

Area of study

This paper is based on faunistic data of the Madrid province, located in the center of the Iberian Peninsula, between the 40° and 41° N parallels and the 3° and 4° W meridians. It is approximately triangle-shaped and has a surface of 8,000 km².

Geomorphologically, Madrid can be divided into two parts: the Sierra de Guadarrama (North) and the Llanos del Sur (southern Plains), according to Hernandez Pacheco (1941).

The Sierra de Guadarrama.- These mountains are included in the Sistema Central, that goes across Madrid province following the main direction of this range, that is from east-northeast to west-southwest, and runs along the north border of the province for 100 km, ranging from 1,000 m (altitude at the surrounding plain) to 2,430 m a.s.l. It is essentially constituted by archaic siliceous rocks (mainly granites and

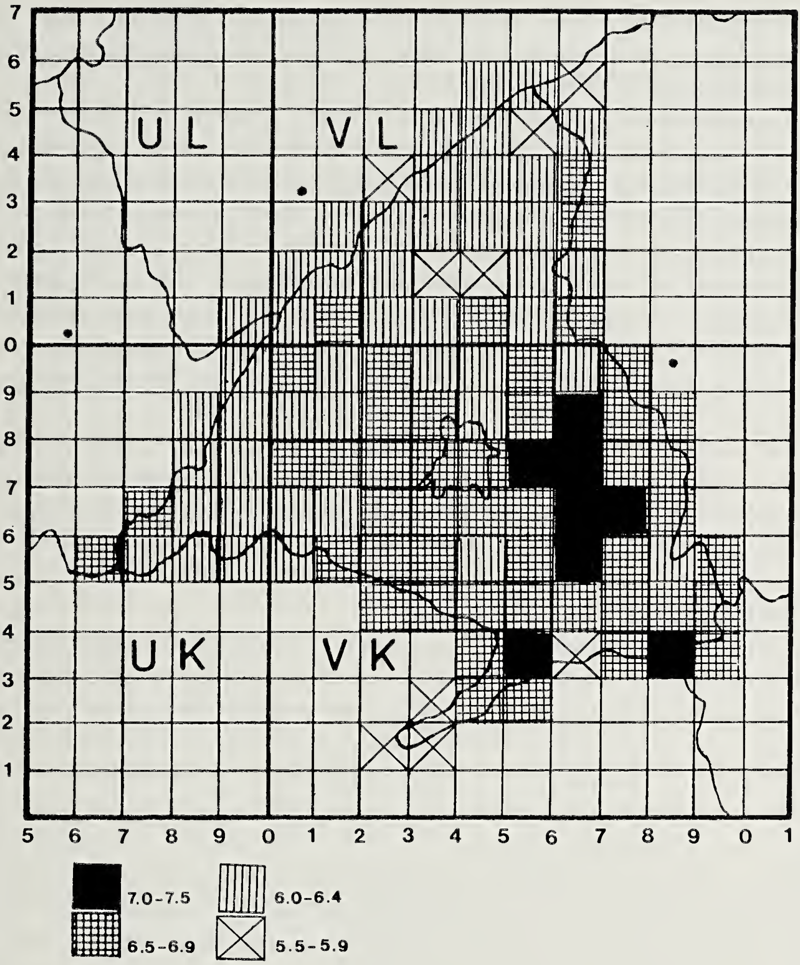

Fig. 3. Map of the Average Chorological Index values in each 100 km² UTM grid in Madrid province.

gneiss), although marly and cretaceous limy lands, miocenic arkosic sands and quaternary alluvial soils are also present. Its climate even inside the general continentality, is more humid and colder than that of the Llanos del Sur, and it is classified as Humid Mediterranean type, following to Emberger (Viejo, 1982). From a botanic point of view, the Sierra de Guadarrama belongs to the Mediterranean Region, Carpetano-Ibérico-Leonesa province (Rivas Martinez, 1982; Izco, 1984) and three bioclimatic levels can be distinguished: Supramediterranean, Oromediterranean and Crioromediterranean.

The climax vegetation of each level is respectively: Holm oak (*Quercus ilex*) and Pyrenean oak (*Q. pyrenaica*) woods, Scottish Pine (*Pinus sylvestris*) woods scattered with Juniper *Juniperus communis*) trees and high mountain alpine meadows. Cattle raising and forestry are widespread land uses in the Sierra.

Llanos del Sur.- Located at the south of the Sierra, it is a wide and flat region. Its altitude ranges from 500 to 1,000 m a.s.l. This region is lightly south-exposed, and the Tagus river traverses it along its southern border. Siliceous alluvial soils (arkosic sands) are dominant on the north and west, as well as evaporitic rocks (loams, gypsums, and pontiensic limestone)are on the south and east. Its climate can be classified between Temperate Mediterranean and Semiarid Mediterranean (Viejo, 1982), being much dryer and warmer than that of the Sierra, increasing in this tendency while going further south. This climate, the substratum and the vegetation establish a transition zone in the meeting region with the Sierra, sharing at this point some features with it. Llanos del sur are included in the Mediterranean Region, Carpetano-Ibérico-Leonesa and Castellano-Maestrazgo-Manchega botanical provinces, and only the Mesomediterranean bioclimatic level is present. The climax vegetation consists of Holm oak and Lusitanian oak (*Quercus faginea*) woods, as well as Mediterranean shrubs, although it is very disturbed by land uses, mainly agriculture and urbanism.

Results and discussion

Figure 2 shows species richness in each square, that ranges from 10 to 102 species. The north of the province has the highest species richness per square. In this area two very rich zones can be distinguished: One on the center and the other on the northeast end (Viejo, Martín & de Silva 1988). Another relatively rich region appears on the southeast, with 60-75 species squares. The mid-province region is rather poor, coinciding with the metropolitan area of Madrid. The highly cultivated Tagus Valley, at the south end of the province, is the poorest region. Comparison between the species richness and climax vegetation maps (fig.1) shows that highest species numbers correspond, to a large extent, with the Pyrenean Oak (*Q.pyrenaica*) and Lusitanian Oak (*Q. faginea*) climax areas, at the north and at the southeast regions respectively.

Figure 3 shows Average Chorological Index of every square, which varies from 5.5 to 7.5. The distribution of this variable is different than that of the former (Species Richness). The highest values correspond to the Mesas del Sureste (southeast Plateaux), climax domain of the Lusitanian Oak, although there are also some high ones on the central and southern areas of the province. Lowest values appear on the most altered areas (furthest south end) and on the Sierra de Guadarrama.

There is an interesting point to comment: Richest squares are not necessarily those with highest Average Chorological Index (correlation between both variables, $r= 0.06$). This is because of the own landscape nature and, consequently, because of the different lepidopteran species that occur in them. The north of the province is mainly cool and humid, and its vegetation corresponds to the phytosociological series of the Pyrenean Oak and Scottish Pine, and these vegetal formations are much closer (as a floristic whole) to those mideuropean-atlantic, than the Holm

Oak, Lusitanian Oak and Kermes Oak woods of the south of the province are, which is a highly Mediterranean area. In other words, there are more species with low chorological index in the northern Mountains than in the southern Plains, given that the environmental conditions on the Sierra de Guadarrama (mainly climate and vegetation) are very close to those on west and Central Europe. On the other hand, endemic species and biogeographically "rare" species (high chorological index) occur in typically Mediterranean biotopes (Baz, 1991).

Note that even farming lands, at least those of non irrigated croplands (olive groves, vineyards or cereal fields), present high Average Chorological Index; that means, many biogeographically interesting species can be found here, even if species richness is not high at all (Viejo, 1985).

Conclusions

Obviously the lepidopterologically interesting areas selection, pointing towards their protection, must be based on deeper studies than just the analysis of the species range UTM maps. But it is also evident that in the meanwhile these maps are the only useful argument to establish possible protected zones. Nevertheless, we consider that species richness is a limited criterion, because if we apply no other criterion, no attention will be paid to areas with a low species richness, but may be sheltering a biogeographically interesting fauna; that means the south of Madrid in the present case. By these reasons, we believe absolutely necessary to deep in the analysis, and applying other criteria as well, such as the biogeographic interest of the fauna (Idle, 1986), easily provided by the UTM maps.

Finally, we want to point out the interest that a rather mideuropean fauna has, inside a tipically Mediterranean environment, feature that increases the peculiarity of Sierra de Guadarrama fauna, at least from an Iberian perspective.

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An unrecognized, now extinct, Los Angeles area butterfly (Lycaenidae)

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Abstract. *Philotes sonorensis* has been regarded as a geographically invariant species. This historic viewpoint is corrected and several geographic variants and patterns of variation are described. A new subspecies, *P. sonorensis extinctis,* is named. The subspecies became extinct in 1967 consequent to an engineering program for water diversion. The relationship of *P. s. extinctis* and parapatric *P. s. sonorensis* are discussed.

Introduction

California not only leads the nation as the trendsetter of fashion, the capitol of entertainment, and the model of buoyant lifestyle, but also as the exterminator of species, including butterflies. "Species" is used here in the context of the federal Endangered Species Act which for invertebrates includes subspecies. Extinction means globally lost, versus extirpation, which refers to extinction in only part of the range.

The first recorded North American butterfly extinction was *Cercyonis sthenele sthenele*, last collected in 1880, followed by *Glaucopsyche lygdamus xerces* in 1943-44. Both were victims of land conversion of the San Francisco sand dunes, dunes which now underlie about half the area of the city and which today are scarcely recognizable. Loss of the Xerces blue was especially unfortunate as its populations were a highly polymorphic complex ranging from the spectacular *xerces* phenotype to that of the surrounding parapatric and widespread subspecies *incognita*. The pattern of variation may have been an ecologic/genetic parallel to the situation described by this paper. In 1958 *Parnassius clodius strohbeeni* was last seen in the Santa Cruz mountains, a possible victim of overcollecting. The next known extinction was the unexplained disappearance of *Argynnis (Speyeria) adiaste atossa* around 1960 (Emmel and Emmel, 1973). This fritillary was formerly abundant in the Tejon Mountains near Los Angeles. After 1983 *Glaucopsyche lygdamus palosverdesensis* of suburban Los Angeles was no longer seen, in spite of intensive attempts by a squad of experienced collectors under the able leadership of Jess Morton (Mattoni, unpublished). The species was lost to a combination of overcollecting, poor weather and habitat fragmentation. The time of the last flight of an undescribed subspecies of *Plebejus saepiolus* in the Big Pine area of the San Gabriel mountains was 1985 (Emmel, pers. comm.). At least two additional species are in imminent danger of extinction: *Argynnis (Speyeria) adiaste clemencei* and *Euphydryas editha quino* (=*wrightii* of authors)(Allen, Brown, Ballmer

& Mattoni, unpublished data). Although neither were seen for several years after 1986, the fritillary was widespread with only a single population of the checkerspot reported in 1990. These last observations are hardly encouraging. Several other species are probably not too far behind. These events were so rapid that no timely help was provided by the listing process under the Endangered Species Act. Between widespread political attacks to weaken the Act and serious understaffing of agencies, the future for biodiversity is indeed bleak.

The list can now be expanded by a previously unreported subspecies which became extinct in 1967. The event passed unnoticed because of an unrecognized systematic situation I will in part rectify with this paper. Failure to formally notice significant geographic variation in *Philotes sonorensis* was perhaps a function of later authors assuming authority of earlier authors who did not notice consistent patterns of variation other than naming one form and one aberration. The species clearly stands apart from all Scolitantidine blues, without apparent sister species, in the monotypic genus *Philotes* . The entire species is almost completely confined to the California Floristic Province (described by Raven, 1988), a trait shared with only eight other butterflies. This isolation, combined with a striking appearance, may have biased observers into overlooking complex variations. However, Langston (1963) broke with tradition and cited a substantial and consistently different appearance of specimens from central coastal California when compared with those from the south, figuring females of each. Langston later (1972) referred to macule and aurora variation in northern California colonies. From his thesis on *Philotes* Shields (1973) noted that Los Angeles County specimens are larger with the females more boldly marked. He found no geographic variation in valve teeth number in males, cited the Mattoni and Seiger (1963) report of intrapopulation variation of UFW postmedian macule number in populations of the San Gabriel Canyon wash, and let the matter rest. During the same time period Fred Thorne (pers. comm.) provided specimens and advised that San Diego County populations from the desert (Sentenac canyon area) and coast (Pt. Loma/La Jolla) were sufficiently distinct to warrant subspecific status. Coastal San Diego County populations no longer exist, although there may be remnants along the northern Baja California coast (Brown and Faulkner, pers. comm.). The species distribution is shown in figure 1.

Inspection of series of specimens from throughout the range shows several distinct sets of wing pattern types which beg further systematic study. With escalating destruction of natural habitat such study should be undertaken soon. While preparing a guide for identification and conservation biology of butterflies of the Los Angeles area (Mattoni, 1990), it was necessary to formally name the unique population described below:

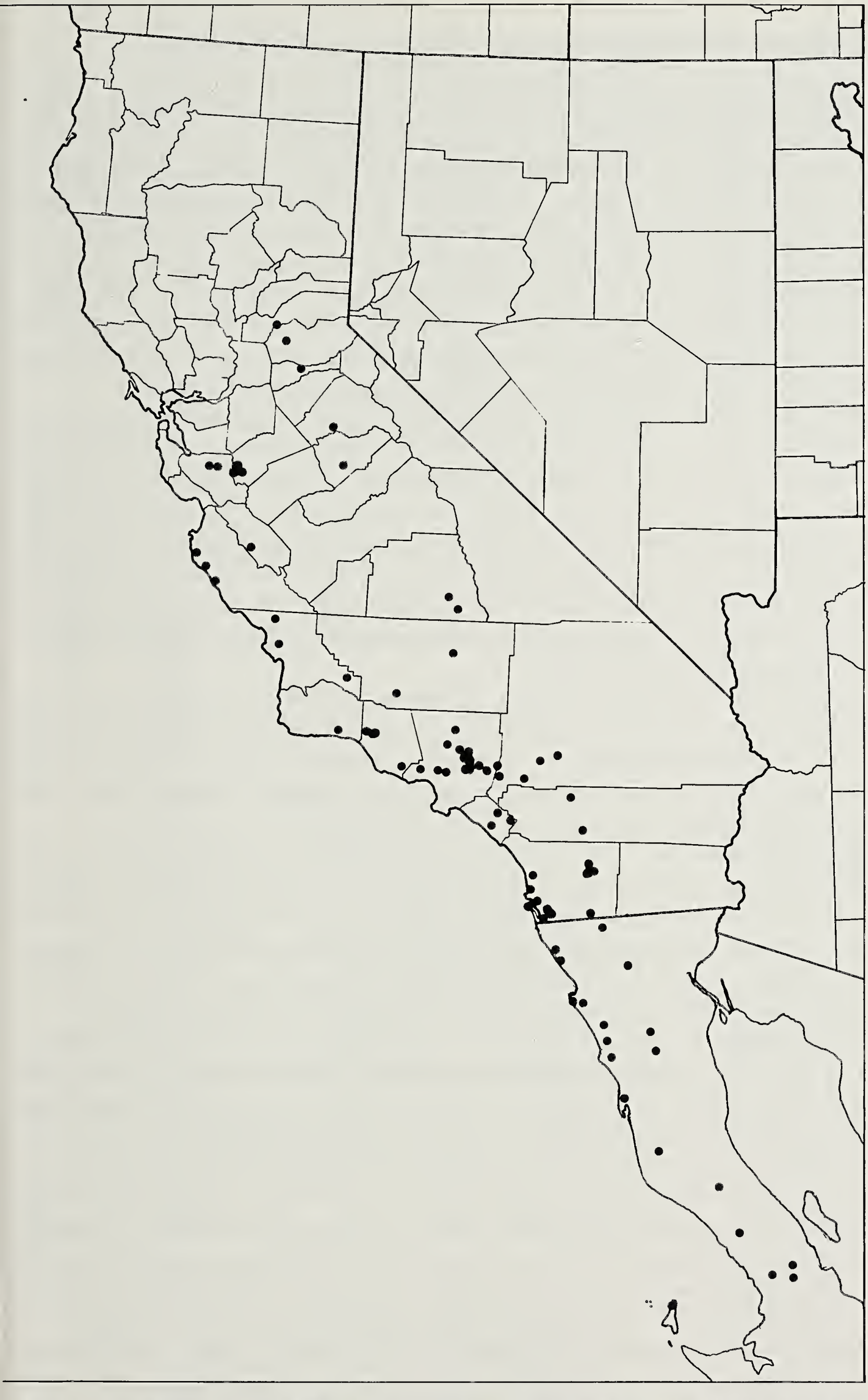

Fig. 1. Distribution map of *Philotes sonorensis*. Data after Shields 1973 with a few recent records.

Philotes sonorensis extinctis Mattoni **new subspecies**

Males. Upperside. Cyanic overlay as in nominotypical species. *Forewing*: postmedian macule number vary in number from none to five, with frequency distribution given in table 1; holotype with four. *Hindwing* as in nominotypical species. **Underside**. Ground medium grey-brown. Fringes well distinguished at all veins. *Forewing*. Macule pattern as in nominotypical species. *Hindwing*. Median space between sub-basal and postmedian macule usually lightened against ground by whitish suffusion, postmedian space darker grey than ground with submarginal macule absent and with submarginal space light grey usually most strongly marked in M_3, Cu_1 and Cu_2. Marginal macules faint.

Females. Upperside. Cyanic overlay similar to nominotypical species, but slightly and uniformly darker due to a higher proportion of melanic scales. Marginal band wider and macules 10 to 30% larger on average than other populations presenting a darker overall aspect. *Forewing*. Postmedian macule number in interspaces Cu_1 and Cu_2 vary from 0 to 3. *Hindwing*. Macules and orange aurora larger than other populations, entire spaces anterior to Rs with melanin suffusion, again presenting a darker overall appearance than nominotypical species. **Underside.** In all aspects similar to males.

Types: All specimens taken in the upper San Gabriel wash from February through April over a period of 1922-1967, after which they were extinct. Older specimens are variously labelled San Gabriel Canyon, San Gabriel Canyon wash, Fish Canyon, and Azusa. Holotype male and allotype female III 24 1963, R. H. T. Mattoni leg.

Type disposition: The holotype and allotype will be placed in the Smithsonian Institution. 115 paratypes will remain in the author's collection until further systematic issues are resolved and will then be placed in an appropriate institution. The Los Angeles County Museum of Natural History has 255 paratypes. All specimens figured will be deposited in the Los Angeles County Museum of Natural History.

Etymology: The subspecies name calls attention to the fate of the taxon. I suggest the common name **Human Folly Blue** because the extinction was due to a short term engineering fix without recognition of long range environmental impacts. The U. S. Army Corps of Engineers destroyed the habitat to provide a spreading basin for ground water recharge. Two consequent ironies of the action are that the Corps of Engineers would today be prevented from such action by its own mandate to preserve riparian habitat and that the groundwater basin being recharged is now contaminated with chlorinated organic chemicals. This historical lesson of environmental tinkering appears forever condemned to repetition.

Nomenclature and Synonymy: C. and R. Felder (1865. Reise Novara 2:281 & plate 35 figs. 3,4) named *Lycaena sonorensis* with the habitat designation of Sonora (Lorquin). The Felder (Lorquin) "Sonora" type locality issue was discussed by Brown (1967). Both O. Shields and J.

	Males X	A	B	C	D	G	I	CM	Sample size	Females 3	2	1	0	CM	Sample size	Total
San Gabriel Mts.																
Wash																
2 (1955)	.005	.60	.13	.07	.19	.01	.005		592	.41	.22	.22	.15		203	795
2 (1956)	.005	.55	.13	.07	.24	.005	.003	.001	733	.39	.16	.16	.28	.008	237	970
4 (1963)		.49			.33				94							
6 Bridge		.50	.18	.05	.27				22	.29	.15	.57			7	29
Total, Wash	.005	.57	.12	.06	.23	.007	.003	.001	1424	.40	.19	.19	.22	.004	447	1871
East Fork	.61	.31			.08				13			1.00			1	14
Coldbrook	.45	.45		.05	.05				20	.17		.67	.17		6	26
Total, mountains	.52	.39		.03	.06				33	.14		.71	.14		7	40
San Diego coast	.31	.57	.04		.08				26	.55	.11	.33			9	35
San Diego desert	.41	.41		.13	.03				39		.12	.82	.06		17	56
Santa Barbara Co.	.13	.72		.09	.03		.03		32	.20		.80			10	42
Atascadero	.08	.46	.21	.04	.21				24						0	24
Alum Rock Park	.32	.45	.19		.03				31		.06	.75	.19		16	47
Del Puerto	.09	.86			.05				22						0	22
Chili Bar	.18	.48	.03	.27	.03				33		.43	.43	.14		7	40

Table 1. Frequency of forewing postmedian macule classes in different geographic populations of *Philotes sonorensis.* Classes are described in text and shown in figure 2. The samples are grouped into the San Gabriel Mountains, which had two distinct phenotypic class populations; the San Diego coast and desert, each with a distinctpopulation; the central California coast; and Chili Bar in the northern Sierra Nevada Mountains. When total sample of female set is less than 6, the class frequency is not scored, but the class size is given (East Fork only). For sample site 4, 1963, only data for classes A and D are available.

Emmel provided additional information (in litt.). A population from "environs de Los Angeles" was named *L. regia* by Boiduval (1869. Ann. Ent. Soc. Belgique 12: 46) but was subsequently synonymized with *L. sonorensis* by Reakirt (1878. Butterflies and Moths of North America). Comparison of published figures indicate the Boisduval specimens differ phenotypically from those of the Felders. Both Felder and Boisduval material clearly was collected by Lorquin, but the exact origin of any of the specimens remains obscure. Two pairs of Boisduval specimens labelled "type" are in the USNM (Oberthur collection). The two well worn Felders syntypes are males in the BM(NH). Photographs of a pair of Boisduval syntypes appear similar to *extinctis*, with the dark postmedian space. The other pair is marked as the widespread montane populations. The specimen figured by the Felders is not *extinctis*, but appears similar the nearby populations and lighter Boisduval syntypes.

Reconstructing the Lorquin type localities revealed the specimens were likely taken in 1852 when Lorquin travelled around Los Angeles and also in San Diego. During travel near Los Angeles he took *Glaucopsyche piasus sagittigera*, most likely near the Verdugo Hills and may well have collected *L. sonorensis* at same time. Neither named taxa conforms to *extinctis*. A type locality must be designated when the species is thoroughly studied.

Diagnosis

The San Gabriel wash population was distinct and deserves special recognition for its combination of three characteristics: 1) postmedian macule pattern frequency and dimorphism of a unique form, 2) complex difference in the underside ground and maculation pattern in almost all individuals, 3) very high population densities.

1). POSTMEDIAN MACULE PATTERN FREQUENCY AND DIMORPHISM OF THE UNIQUE FORM "COMSTOCKI"

The postmedian macule patterns were arbitrarily designated by letter for males and number for females and are illustrated in figure 2. The male classes X, A, B, C, D, G, and I represent a decreasing macule number in interspaces Rs to Cu 1 ranging from 5 to 0 macules. Classes B and C both have 3 macules but different positions. The female classes range from 3 to 0 macules within interspaces Cu 1 and Cu 2.

The form "comstocki" (CM) is illustrated in figure 2, second specimen in row 3 and Mattoni (1964: specimen 15). On the upperside, male CM are indistinguishable from "normal" specimens that are without macules (pattern class I), but the underside is obviously distinct. The ground is entirely the darker grey that is restricted to the postmedian interspace in the normal. The hindwing macules are absent and the forewing postmedian macules are aggregated into a single discoidal macule. Female CM undersides are as the male, but the upperside forewing macules are distributed as on the underside. The CM character state was

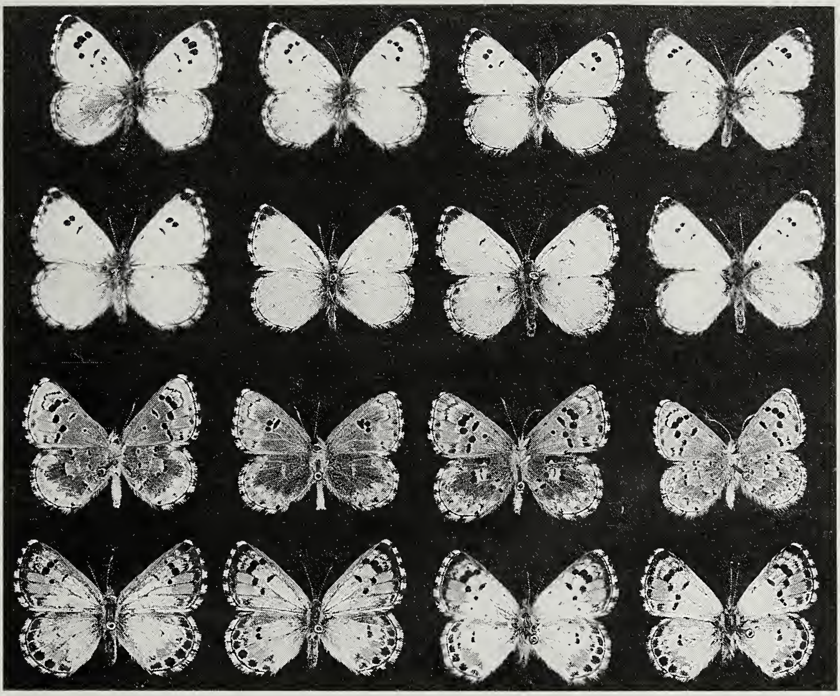

Fig. 2. Specimens of *P. sonorensis extinctis* from San Gabriel Canyon wash showing classes of upperside pattern and underside variation. Left to right. Row 1, males: X, A, B, C; row 2, males: D, G, I (or CM, difference in underside), asymmetric, D on left, B on right; Row 3, undersides: wild type, CM ("comstocki"), D/CM, upper San Gabriel canyon; row 4, females: 0, 1, 2, 3. See text for further explanation. Unless otherwise stated all specimens in figures leg. R. Mattoni.

probably controlled by a recessive gene that modified melanin deposition at a critical stage during pigment formation in the pupa. The hypothesis that the CM variant was environmentally induced cannot be discarded, yet failure to observe CM in any other populations and its relatively high frequency at San Gabriel strongly supports a genetic explanation. Recessiveness is inferred from a report of all wild type progeny from a CM female by an early collector, but both report and undocumented data are hearsay.

Following the conclusion of their fieldwork, Mattoni and Seiger (1963) noted an additional distinct variant class: rare males with state D upperside macule pattern and females with a 0 macule pattern, but with a underside primary postmedian macule series less than half the distance from the discoidal macule to the distal wing margin. This variant (D/CM) is illustrated by specimen 11 in figure 2, 13 in figure 3, and specimens 13, 14, and 20 in Mattoni (1964). Our hypothesis was that this variant represented the heterozygote of CM, as its frequency approxi-

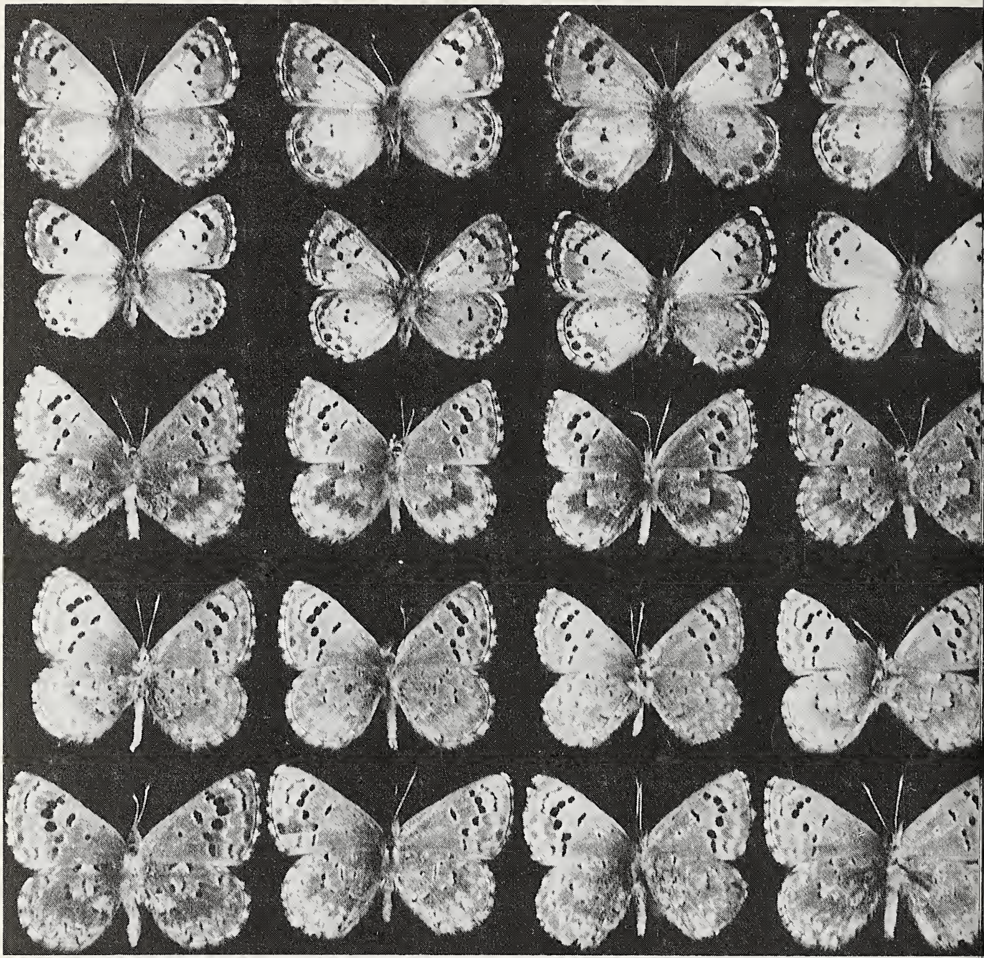

Fig. 3. Variation in upperside patterns in females and underside patterns comparing specimens from lower San Gabriel canyon wash (*extinctis*) and upper San Gabriel canyon (*sonorensis*). Row 1, females, wash. Row 2, females, upper canyon at Coldbrook ranger station. Row 3, undersides, wash. Row 4, undersides, Coldbrook ranger station. Row 5, undersides, fire road or site 7, intermediates, see text.

mated the Hardy-Weinberg equilibrium in the small sample we made in 1963. Mattoni (1964) published a color plate illustrating these forms as well as samples from other populations. The legend for this plate is given below, as this information is not elsewhere available.

The frequency of all the postmedian macule classes and CM are given for populations from which more than 20 specimens were available. It should be noted that asymmetry is exceptional. The 14-specimen East Fork sample was included to increase the upper San Gabriel canyon population. Three conclusions can be drawn from these data: wash population (*extinctis*) males had a significantly greater frequency of class D (except Atascadero) and a significantly lower frequency of class X than any other populations, wash females had a higher frequency of class 3

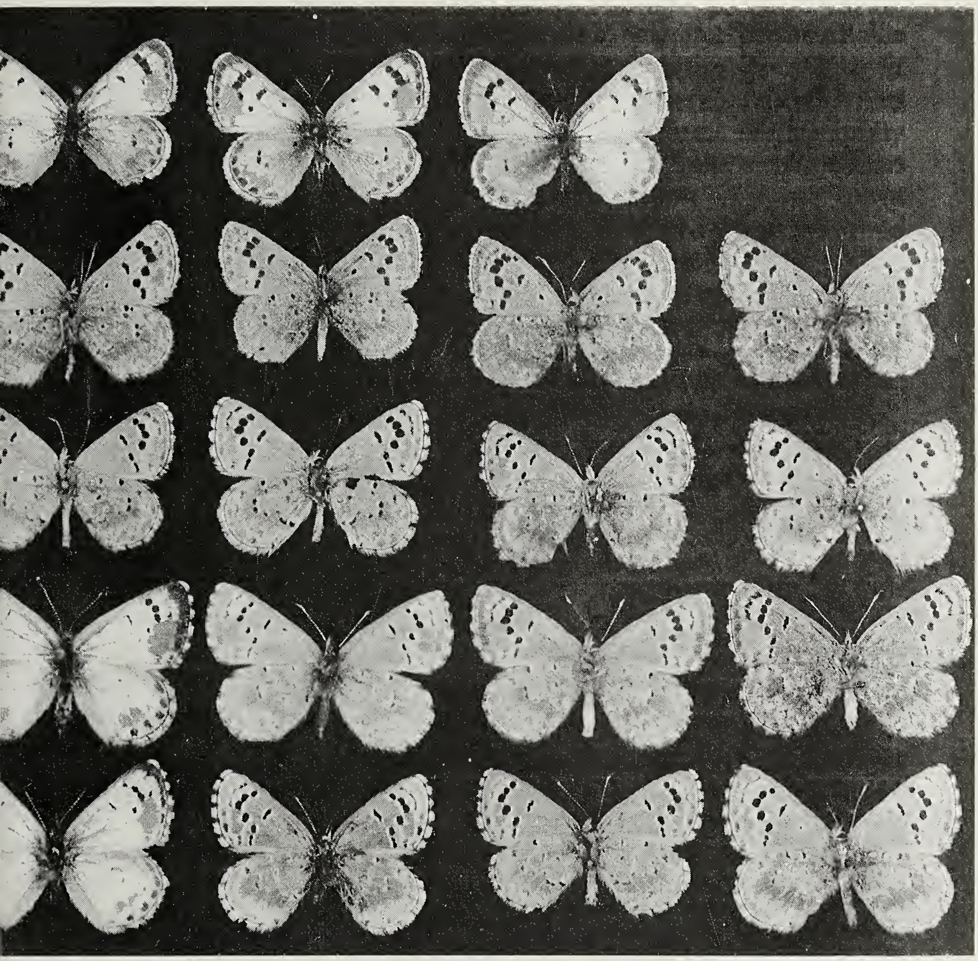

Fig. 4. Specimens representative of different geographic areas. Row 1, females, El Dorado county, Chili Bar, leg. O. Shields. Row 2, undersides, same data as row 1. Row 3, undersides, Santa Clara county, Alum Rock Park, leg. R. Langston. Row 4, female and 3 undersides, San Diego county, Sentenac Canyon, leg. F. Thorne. Row 5, female and 3 undersides, Santa Barbara county, Santa Barbara, leg. R. Denno.

than any population (except San Diego coast, possibly representing a sampling error, but see below), no valid specimen of CM has ever been observed from any but the San Gabriel canyon wash population. Since the extinction of *extinctis*, local collectors mostly take their specimens from other parts of the San Gabriel mountains, usually in Brown's Gulch, located 3 miles north of what was the wash. Form CM has never been seen in spite of a thousand or more takes in the vicinity. A specimen of CM reported by Shields (1973) from Ventura County (Henne, leg.) was apparently a class I specimen in which the underside was not inspected. The Henne collection in the LACM has a Ventura I male with a normal underside.

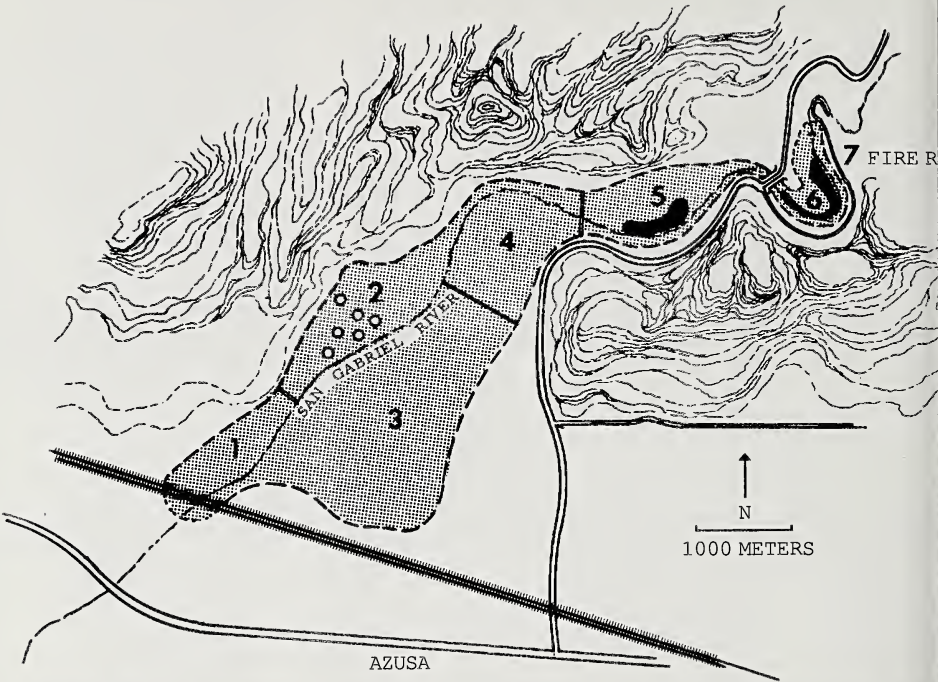

Fig. 5. Map of distribution of *Philotes sonorensis* in the lower San Gabriel wash prior to 1967. Areas in black remained in 1968, although no butterflies remained. These last remnants destroyed in 1980's.

2). THE UNDERSIDE PATTERN COMPLEX

Virtually every specimen from the wash population can be separated from the populations in upper San Gabriel canyon and most other localities by the underside pattern. The character is illustrated in figures 2, 3, and 4 as well as Mattoni (1964). The difference between the wash and upper canyon populations is most striking in figure 3, comparing rows 3 and 4. The border between these character states is abrupt, the limit apparently having been the edge between the wash and the steep slopes marking the beginning of the canyon walls. This border is shown on the map, figure 5. Butterflies taken at this interface are shown in figure 3, row 5. The specimens taken here, which were rare, indicate a zone of intergrades and segregates. Since early 1980 access to the area has been blocked, so status of the species is unknown at the site.

The distinct dark grey postmedian space on the secondaries occurs in coastal San Diego county populations (extirpated, see Mattoni 1964 figure 21) and some other alluvial washes from the south slopes of the San Gabriel mountains. The latter have not been well sampled and today few, if any, remnants of these wash populations are extant.

Samples of underside patterns from other populations are illustrated for comparative purposes. These include desert San Diego county figure

4, row 4 and Mattoni 1964, 29-32), Santa Barbara (figure 4, row 5 and Mattoni 1964, 25-28), Alum Rock Park, Santa Clara county (figure 4, row 3), and Chili Bar, El Dorado county (figure 4, row 2). The Chili Bar population is also singular in that 90% of the sample lacked checkered fringes.

3). HIGH POPULATION DENSITIES

The reason the San Gabriel wash was the long favored locality of collectors of the Human Folly Blue was the extremely high population numbers of the butterfly in the small circumscribed area where it occurred (figure 5). The 1955 and 1956 study of Mattoni and Seiger (1963, and unpublished) indicated total standing populations in those years on the order of tens of thousands in the 8 square kilometer area the population inhabited. During the period beginning with the discovery of the population until its destruction in 1967, collectors could easily take several hundred specimens in a day. No other known population of the species had or has the potential of such yields. Abundance of individuals of the *extinctis* population was unique in terms of high densities in every year for which records are available. The density characteristic was not a function of foodplant density, as many other populations (i.e. Baja California, central California coast) are found in regions where *Dudleya lanceolata* and *D. cymosa* are among the dominants in their plant communities yet the butterfly remains rare.

Rarity has only recently been viewed from the standpoint of relating the characteristics of species that define rareness (Rabinowitz, 1981). Through most of its range *P. sonorensis* is rare in the sense of being constantly sparse yet occurring across several limited habitats. Under all conditions it is distribution limited by the occurrence of its foodplant, usually a colonial and local plant. Because butterflies are all *r*-strategists, excepting possibly the giant *Ornithoptera*, rarity must have an ecological and/or genetic bases. All populations have the potential of rapidly achieving high density, but do so only on occasion. The very dense population of *extinctis* occurring adjacent to, and probably interbreeding with, low density *sonorensis* implies a gap in adaptive characteristics. Populations of the species from the nearby Big and Little Dalton, Santa Anita and Eaton washes occur(red) only in low density and without the diversity of forms found at San Gabriel.

Microgeographic distribution and systematic implications

The wash population distribution as known in 1963 is mapped in figure 5. At that time there was undisturbed wash habitat to the south of the extant population, but no butterflies could be found although foodplant was present. The areas to the east of 3 and west of 1 had been denatured by residential construction. It is unknown if the butterfly ever occurred in these sites. The black overlay denotes undisturbed sites remaining in 1968. Both were scouted in that year without finding specimens, al-

though a few were taken on the fire road, where they must still occur, but is now inaccessible. These last sites were denatured by construction and clearing in about 1980.

Site 7 (fire road) referred to all the steep slope east and north of site 6 and the bridge. The flat wash immediately north of 6 is an orchard. At this point the road was located within a few feet of the river and it was possible to walk about a mile upriver. Although foodplant was present over this entire area, the butterfly was uncommon. Specimens sampled in site 6 were all of the *extinctis* pattern. The sedentary nature of the species (Mattoni and Seiger, 1963 and unpublished; Keller, Mattoni and Seiger, 1966) probably limited movement across the river between sites 6 and 7. To what extent the distinct patterns and characteristics of *sonorensis* and *extinctis* were maintained by selection as opposed to loss by hybridization remains unknown.

Coda

The *Philotes sonorensis sonorensis / extinctis* relationship had the potential of providing a fascinating case for investigating evolutionary biology in sedentary butterflies. The contrast of two adjacent populations with different complex wing patterns, clear-cut polymorphisms, and ecologies presented a singular situation. Destruction of the wash habitat and attendant extinction of *extinctis* co-opted further investigation. Yet at some future time, when human species density is of necessity reduced and constrained by resource limitation, and the San Gabriel river dams no longer function due to siltation, the wash habitat may be revegetated and a population of the butterfly could re-invade the current biological desert. Should curiosity of biological matters survive for future humans, this note may be useful.

Acknowledgements. The original manuscript was substantially rewritten and vastly improved following input and sometimes pungent comment from Mike Collins, John Emmel, Tom Emmel, Merrill Peterson, Barry Prigge, and Oakley Shields. W. D. Field of the Smithsonian Institution generously provided photographs of one pair of the *regia* types. Chris Henne translated the Boisduval description from the French.

Legend for Mattoni (1964). Specimens read left to right. Top five rows, all San Gabriel Canyon wash 1963, Males wing pattern class: 1, C. 2, B. 3, A. 4, X. 5, Female "comstocki" (CM). Males: 6, I. 7, G. 8, D. Females: 9, 3 10, 2. 11, 1. 12, 0. Undersides: 13, D/CM?. 14, D/CM?. 15, CM. 16, Female, darkly marked. Undersides: 17-19 variants of wild type. 20, D/CM?. 21, San Diego, Paradise Valley (Fred Thorne, leg.). 22-24, Upper San Gabriel Canyon, East Fork (Mattoni, leg.) Underside, 22. Female, 23. Male, 24. 25-28, Santa Barbara, (R. F. Denno, leg.). 29-32, San Diego Co., Sentenac Canyon (Fred Thorne, leg.).

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28(4):310-315, 1989(91)

Notes

Gesneriaceae as a larval hostplant of *Hyposcada virginiana* (Nymphalidae: Ithomiinae)

Knowledge of the hostplant interactions within the subfamily Ithomiinae have been important to our understanding of neotropical butterfly evolution and ecology (e.g., Mielke & Brown 1979; Gilbert 1983; Ackery & Vane-Wright 1984; Brower 1984; Boppré 1984; Brown 1987; DeVries & Stiles 1990; Vasconcellos Neto 1991). Broad patterns of hostplant use in the family Nymphalidae are well known, and it is clear that the Ithomiinae is largely composed of specialists on the Solanaceae, with a few species that use the Apocynaceae (Drummond & Brown 1987; DeVries 1986, 1987; Ackery 1988). There is, however, one frequently cited exception to the overall pattern of ithomiine hostplant interactions: Haber (1978) reported that Costa Rican *Hyposcada virginiana evanides* Haensch may oviposit on the genera *Columnea* and *Drymonia* (Gesneriaceae).

The potential use of Gesneriaceae as a larval hostplant by any member of the Nymphalidae is singular. In fact, the only records of Gesneriaceae in the extensive, world-wide review of nymphalid hostplants by Ackery (1988) are those of Haber (1978). In conflict with Haber's records (but in line with other ithomiine host records) are observations by Drummond & Brown (1987) that Brazilian *Hyposcada egra* (Hewitson) oviposited on a plant thought to be *Markea* (Solanaceae), and that the larvae were reared in the laboratory on *Juanulloa* (Solanaceae). Thus, with our understanding of nymphalid hostplant relationships in general, and those of the Ithomiinae in particular, there is need for verification or rejection of Gesneriaceae as a hostplant of *Hyposcada* (DeVries 1986, 1987; Drummond & Brown 1987; Ackery 1988). Here I provide the first direct field corroboration of Haber's (1978) suggestion that *Hyposcada* uses Gesneriaceae as a larval hostplant.

On 12 April 1990 at 0810 hrs I observed a female *Hyposcada virginiana* oviposit 3 eggs on the underside of an intermediate age leaf of *Drymonia* sp. (Gesneriaceae) at Jardín Botánico Wilson, San Vito de Java, Costa Rica. The woody, hemiepiphytic plant with glabrous, semi-succulent leaves, was attached to the side of a palm tree approximately 5 m above the ground, and was in shade at the time of oviposition. Each oviposition act was separated by about a 30 second interval, and the eggs were deposited near the middle of the leaf. The white eggs were large for an ithomiine ($\approx$ 2 mm diameter), bore a sculpturing that could be detected without the aid of a lens, and were slightly wider towards the micropylar region than the base. First instar larvae (body entirely pale grey with shiny black head, and no tubercles) hatched 5 days later, ate the egg shell, rested for 24 hours, and then began eating small, round holes in the leaf. Second, third, and fourth instars bore no projections or papillae, all were shiny, semi-transparent grey with a dull yellow band at the interface of venter and lateral areas that extended from segment A-8 to T-1, continuing across the anterior margin of T-1. In all instars the head was shiny black, and without patterns or relief. Although all three larvae were healthy and growing vigorously, a necessary move to a different field site where no acceptable hostplant occurred prohibited rearing them beyond

fourth instar. The larvae were preserved in ETOH and specimens are in both the author's voucher collection and that of the Museo Nacional de Costa Rica.

None of the larvae fed at the leaf margin, but as is typical of many ithomiines that feed on Solanaceae, they ate round holes in the interior of the leaf blade, then moved to another undamaged section to eat another hole. The larval feeding behavior left the once entire *Drymonia* leaf with a large number of irregular holes. The larvae were cryptic while on the plant and fell into what Ackery (1988) pointed to as the typical Solanaceae feeding type of ithomiine. A casual inspection of 10 other *Drymonia* sp. plants in the area showed that most of their leaves had feeding damage similar to that caused by *H. virginiana* larvae. However, I found no other *H. virginiana* larvae at this or subsequent inspection over an intermittent three month period.

The observations here raise three points. First, although it is unknown whether the *H. virginiana* larvae would have produced adults, the present observations support Haber's (1978) records that Gesneriaceae is a hostplant for Costa Rican *Hyposcada*. Secondly, the general vegetative similarity between some hemiepiphytic Solanaceae (i.e., *Markea*, *Juanulloa*) and some hemiepiphytic Gesneriaceae (rounded, glabrous, semi-succulent leaves) allows for the possibility that the *H. egra* oviposition record (Drummond & Brown 1987) was actually on a Gesneriaceae. Finally, when the observations of Drummond & Brown (1987) and those here are considered together, they suggest the possibility of some chemical similarity between Solanaceae and certain Gesneriaceae.

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Manifesto on Conservation

Editor's note:

The Lepidopterological Society of Japan held its first seminar on the conservation of butterflies in June 1990. The conveners drafted, and the members present passed, a resolution on conservation. This resolution was provided by Prof. Atuhiro Sibatani and is published in its entirety below.

This action by the Japanese Society is a highly significant event. It makes a strong statement on behalf of a large grassroots body of both professional and amateur biologist members in a leading industrialized nation. It is a particularly remarkable document given its origins in a country heretofore notorious for neglecting environmental concerns in favor of immediate economic benefit. The thrust of the resolution correctly emphasizes the need to protect total biodiversity while minimizing the importance of individual species. We publish this as a model statement for many circumstances.

Manifesto

A statement developed at the first seminar on *The Conservation of Butterflies as a Part of Nature*, 2-3 June 1990, Osaka, co-sponsored by the Lepidopterological Society of Japan and the Osaka Museum of Natural History.

Participants at the first seminar of the Lepidopterological Society of Japan (LSJ) have confirmed the following statements.

- The first cause of nature conservation shall not be the protection from extinction of individual species, but preservation of diversity in biological communities and ecosystems.
- This means to maintain, along with persistent diversity of individual gene pools and species, the integrity of systems which may well entail local alterations of these systems.
- Butterflies are pertinent bioindicators of the terrestrial ecosystem. Hence, the conservation of butterflies implies conservation of the entire ecosystem.
- In order to fulfill the objective of nature conservation, we are responsible and willing to work responsibly, not only to maintain nature's biodiversity, but also to restore this diversity in Japan as well as the world at large, under cooperation with other bodies and using butterflies as indicators.

Implications and further explanation

I. The Position of the LSJ

A. Since 1965, LSJ has engaged in activities for conservation of the Japanese Lepidoptera (mainly butterflies) by setting up the Committee for Study of Nature Conservation Issues (since 1975 the Committee for Nature Conservation) and by issuing occasional announcements and appeals. The society also edited and published *Decline and Conservation of Butterflies in Japan I* (1989/90). With this publication, LSJ demonstrated in advance of other national bodies concerned with insects, its interests in and responsibilities for the conservation of butterflies and shed light on some of the problems of butterfly conservation. We must admit, however, that LSJ has lagged behind related organizations in Europe and America. Our failure to establish reliable principles about the possible relationship between butterfly conservation and collecting as well as scientific studies thereof, may account for this lag.

B. Fortunately, along with the growth of scientists' concerns in problems of both domestic and foreign nature conservation, we have witnessed significant progress in the theory of butterfly conservation which has profoundly extended our understanding of the larger issues. We now wish to present, on the basis of our accumulated experience and the recent theoretical advances, the following plans for concrete action:

1. To hold, for several years, and every year if feasible, seminars, international symposia, etc. on conservation of butterflies in order to examine general theories of conservation as well as concrete means to counteract decline and extinction in individual cases, and also to work out guidelines for actions and practice.

2. To compose guidelines for butterfly collecting and investigation. Until its completion the relevant clauses in the corresponding codes of the Royal Entomological Society (U.K., 1968) and the Lepidopterists' Society (U.S.A., 1982) should be consulted for ethical norms.

3. To compile, as soon as possible, estimations of the danger and threat of extinction for all the butterfly species of Japan and suggestions for concrete actions to be taken for their protection and, where applicable, eventual local reestablishments.

C. Although opinions expressed herein were supported at the first seminar of LSJ, they do not necessarily represent opinions of the Society as a whole. Endeavors will be made to have this manifesto endorsed by the Society.

II. Scientific Understanding of Butterfly Conservation.

A. Butterflies have a high reproductive capacity, generally undergoing large fluctuations of population size in nature, but being capable of recovery from serious declines of population density. Ordinary, disciplined, modest collecting does not threaten sustained survival of any butterfly populations unless their habitats are destroyed or disturbed for other reasons.

B. The concept that butterflies can be used as significant indicator organisms for terrestrial ecosystems has been adopted in many countries. We also agree with this attitude. Today butterfly conservation does not simply imply butterfly preservation alone, but has become an indispensable means to maintain the persisting diversity of terrestrial ecosystems at large.

C. The decline and extinction of many butterfly populations, as witnessed in recent years in Japan, has largely been the consequence of the loss of habitat

caused by the recent rapid and profound structural alteration of industry and the extensive development which occurred in parallel with it. Fortunately, there has been no record of extinction of butterfly taxa (species and subspecies) in Japan yet. However, danger of complete extinction may be imminent for some taxa.

D. At present, the most endangered species are those which inhabit rural modified environments closely situated to human residences.

E. Because of these circumstances as well as for the reasons described in C, we wish to point out that the policy of butterfly conservation as adopted by the state and local governments in Japan and many other countries, comprising prohibition of collecting at either specific or population level, with occasional inclusion of protection of the habitat, has not properly served the newly defined purpose of conserving the persistent diversity of butterflies or ecosystems.

F. Butterflies are components of diverse ecosystems. Reasons for their decline and extinction are complex and far from uniform, varying from species to species and even from population to population within one species. Protecting butterflies from extinction accordingly requires scientific analyses at various levels, for which continued training of young butterfly workers, capable of undertaking scientific surveys in the field is needed, as well as education of the general public.

III. Nature Conservation in General

A. In natural ecosystems species diversity is generated and maintained by interactions among numerous and complex components. While individual ecosystems give rise to persistent diversity, they undergo perpetual alterations to their component species and the size of their populations. Moreover, it is these alterations which provide the mechanism enabling the maintenance of diversity. For this reason, the temporary conservation of a particular species within a small area is sometimes incompatible with securing species diversity in an ecosystem. Since ecosystems are usually undergoing a process of perpetual change and transition, human interference is necessary to keep them "stable" or constant.

B. Traditional agri- and silviculture and natural disasters are two main external causes of "sound" changes in ecosystems. They do this by interrupting vegetational succession at various stages resulting in rejuvenation, therein guaranteeing species diversity. Thus, before the advent of modern civilization, traditional society and culture were integral parts of the mechanism by which diversity of the ecosystem was perpetuated. Today the situation is completely changed. New industrial structures have either destroyed the natural environment or affected its simplification with the calamitous loss of factors which generated the previously extant diversity. The recent impoverishment of the butterfly fauna reflects this very well.

C. A highly desirable conservation policy would not consist of promoting a list of species whose collection is formally prohibited, but would aim at providing safety for *all* the butterfly species occurring in individual regions and localities. However, since natural environment is in constant transition, such a policy should not imply an unnatural fossilization of the current situation, but should aim at instituting both natural and cultural mechanisms to enhance biodiversity through modest man-made (or human-sized) interference with the system. The usual practice of environment impact assessments which refer to the *status quo* as a criterion for preservation, does not serve the objective of nature conservation. Official bodies and grass-roots movements active in nature conservation are at a turning point where they should reappraise the nature of the problems they are faced with in order to achieve the goals to which they aspire.

An Attractant for *Zerene eurydice* (Pieridae)?

During the summer of 1981, while living in an apartment near the campus of California Polytechnic State University, San Luis Obispo, I observed unusual behavior of *Zerene eurydice* (Boisduval) toward a hedge of the cultivated shrub called xylosma, Xylosma congestum (Lour) Merrill (Flacourtiaceae). Throughout the summer, especially during August, males and females of Z. eurydice were commonly seen in westward flight which took them over or around the hedge of xylosma. One day the hedge was trimmed to shape by gardeners and the clippings were left on the ground next to it. During the next two weeks or so after the trimming, individuals of both sexes of Z. eurydice would approach the hedge in their normal manner, but once within about one meter from the shrub they would drop down to alight on the clippings. None were noticed to extend their proboscis or move any part of their body; they remained motionless with wings folded as if basking in some welcome scent. If allowed to remain undisturbed, the butterflies would return to flight after about 3 minutes with no apparent effects. Attempts to approach the butterflies startled them and they took flight. No less than eight individuals displaying the behavior were counted and recorded; others were casually noticed, but were neither recorded nor captured. This behavior ended about two weeks after the hedge was trimmed, possibly because of evaporation or decomposition of compounds within the xylosma clippings.

The cause of such behavior is a mystery, but perhaps involves attractance to chemical compounds within the plant; xylosma gives off a characteristic odor especially after it has been trimmed. Two other reported attractants for Z. eurydice are purple flowers (Emmel, T.C. & J.F. Emmel, 1973, The butterflies of southern California, Natural History Museum of Los Angeles County, Science Series 26: 1-148. See page 20) and fresh horse manure (Garth, J.S. & J.W. Tilden, 1986, California butterflies, California Natural History Guides: 51, U.C. Press, Berkeley. See page 110). Once isolated, the chemical(s) in Xylosma might prove to be a worthwhile attractant for Z. eurydice; more reliable than finding purple flowers and less offensive than horse manure!

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Book Reviews

BUTTERFLIES OF EUROPE. Vol. 2. INTRODUCTION TO LEPIDOPTEROLOGY. 1990. Otakar Kudrna (ed.). AULA-Verlag, Wiesbaden, 557 pp., 93 figs., 4 col. pls., 25 tables, 2 diagrams. ISBN 3-89104-033-4. Available from: AULA-Verlag GmbH, Postfach 1366, Luisenplatz 2, 6200 Wiesbaden 1, Germany, Price: 248 DM.

This is the third volume to appear in the eight volume series *Butterflies of Europe* and is intended as a text and reference book for advanced students.

Ch. 1 is a short introduction by O. Kudrna. Lepidopterology is the study of Lepidoptera from different viewpoints such as taxonomy, ecology, physiology, cytology, behavior, etc.

Ch. 2, Lepidopterology in Europe, by Kudrna and M. Wiemers, is an address guide to major European museums, institutes, and societies possessing important collections and libraries. BMNH has the largest butterfly collection and the best entomological library in the world. Also included are current European Lepidoptera journals and a "Who's Who" of over 300 "great" European lepidopterists, complete with obituary references and collection depositions.

Ch. 3. early stages, by J. P. Brock gives general characteristics, keys to families for larvae and pupae, detailed line drawings of morphology, and a brief account on preserving early stages.

Ch. 4, adult structure and function, by J. A. Scott, discusses internal and external morphology with the aid of numerous labelled drawings. It also covers breathing and blood circulation; feeding, digestion and excretion; and nervous, sensory, and endocrine systems.

Ch. 5. butterfly phylogeny and fossils, by Scott and D. M. Wright, reviews chemical-genetic, intuitive, phenetic, biological species, and cladistic methods of phylogeny study. There is a good discussion of cladistic methods which they apply in the remainder of the chapter. Sections list synapomorphies for Pyraloidea-Macrolepidoptera, Macrolepidoptera, Hedyloidea-Hesperioidea-Papilionoidea, and each Rhopalocera group at the family, subfamily, and sometimes tribal levels. The outgroup for Hedyl.-Hesp.-Pap. is not specified but is probably most Ditrysian moths. They accept Hedylidae as the sister-group to all butterflies. A cladogram of subfamilies and some tribes is presented, calculated by hand from the character data, though it is difficult to see how the most parsimonious choice was made given the large number of taxa (cf. Felsenstein, 1978, Syst. Zool. 27: 27-33). Showing the distribution of the specific characters on the cladogram would have clarified the analysis for the reader (cf. de Jong, 1983, Zoologische Mededelingen 57: 243-270; Nielsen, 1987, Invertebr. Taxon. 1: 201-229). Their data also should be run on a computer for more objective results. In their view, the frenulum of *Euschemon* is the expression of a suppressed gene rather than an indicator of primitiveness. Also, they show Lycaenidae evolving from the ancestor of Nymphalidae via ancestral Riodinidae, implying foreleg reduction reverted to a normal foreleg condition in Lycaenidae. It is unclear how they determined that the listed synapomorphies only apply to each group in question and are absent in all the remaining groups. This is the most comprehensive cladistic analysis of butterflies yet attempted, but butterfly fossils are all too briefly discussed in less than a page and are not updated since the late 1970's.

Ch. 6. origins and phylogeny of butterflies, by Brock, considers phenetics and cladistics as "bogus" and heavily criticizes Scott's work. Cladistics is not without controversy, but personal vendettas have no business being aired in an introductory text. He discusses character correlations and notes that characters used in higher level classification are largely stabilized by canalization and that parallelism has introduced confusion into Lepidoptera phylogeny schemes. He discusses butterfly characters in relation to those of moths and from this limited set of selected characters arrives at conflicting conclusions: that butterflies arose from Microlepidoptera *and* Hedylidae by monophyly! However, butterflies may be diphyletic (Shields, 1989, Tyo to Ga 40: 197-228) or even triphyletic if Hedylidae is another entry-point. There is some discussion of only two other proposed theories: ancestry from Pyraloidea and cossid-castniid. I believe he is correct in questioning Scott's papilionid-pierid eleven "shared" traits. Numerous differences between papilionids and pierids (e.g. egg, pterin array, osmaterium, aorta, *Baronia* immatures unlike pierids, etc.) should not be ignored even though they are autapomorphies since they add up to major differences.

Ch. 7, genetics of European butterflies, by R. Robinson, discusses inheritance, epistasis and hypostasis, genes, multiple alleles, inviability and impenetrance, gene linkage, polymorphism, electrophoretic and quantitative variation, cytogenetics, chromosome number variation, chiasma, centromeres, sex chromosomes, sex chromatin, and supernumerary chromosomes, with a section on genetics of selected species. A table lists haploid chromosome numbers that are known for ca. 60% of European butterfly species with references. The text, however, is difficult to follow for the non-devotee (such as myself).

Ch. 8, case studies in ecological genetics, by P. M. Brakefield, defines ecological genetics as "an integrated study of ecology and genetics concerned with understanding evolutionary processes," e.g. industrial melanism. Case studies include eyespots in *Maniola jurtina* and *Coenonympha tullia*. He also describes methods, field surveys, and genitalia variation.

Ch. 9, butterfly chromosomes and their application in systematics and phylogeny, by Z. Lorkovic, is based mainly on the classical paraffin-cut method which requires little lab assistance. Special attention is devoted to illustrations, mainly drawings, of the numbers, sizes, etc. of chromosomes and their significance in phylogeny. Discussions include spermatogenesis, oogenesis, fission and fusion of chromosomes, supernumerary chromosomes, individual variation of chromosomes, behavior of chromosomes in hybrids, and significance of karyotypes for taxonomy and phylogeny, along with a section on procedures, methods, and techniques for chromosome number frequency for European butterflies. This chapter is clearly and concisely written — a model summary. He suggests that chromosome numbers do not support an intimate relationship of Satyridae with Nymphalidae and Riodinidae with Lycaenidae. There are two color plates of hybrid pierids.

Ch. 10, enzyme electrophoretic methods, by H. Geiger, summarizes electrophoresis methods as applied to butterflies. Electrophoresis is not for amateurs since a well-equipped lab and special training are mandatory. Electrophoresis is a useful tool for analyzing problems in systematics and evolutionary biology. He also discusses analysis of enzyme electrophoretic data, steps in drawing dendrograms, relevant mathematics, and the method's disadvantages.

Ch. 11, experimental breeding of butterflies, by S. R. Bowden, notes that experiments can determine if varieties are due to environment or are genetic. He covers hybridization, fertility, pairing cages, growing nectar flowers, larval

housekeeping, breeding synchronization, sex-ratio, and record keeping. Fresh material is often needed in electrophoresis and chromatography. There are two color plates of genetic forms of the *Pieris napi* group. This chapter is quite brief and is highly critical of cladistics.

Ch. 12, parasitoids, by M. R. Shaw, covers Hymenoptera and Diptera that attack the early stages of butterflies. He notes they are little studied and that misidentifications abound. He also discusses parasitoid biology, difficulties encountered in their study, an outline of the principle groups, collecting and rearing techniques, labelling, and transport. Their host associations can be phylogenetic or ecological in nature.

Ch. 13, butterfly behavior, by T. G. Shreeve, discusses thermoregulation, mate-location, mate-recognition, egg-laying, and feeding and their methods of study, though no mention is made of such topics as roosting, fear flight, etc.

Ch. 14, butterfly movements, by Shreeve, is divided into movement, dispersal, and migration and is often theoretical. Books devoted to migration are not mentioned.

Chapters 3, 4, 7, and 12 have glossaries of terms and there are many useful references cited in most chapters. The book begins with a comprehensive table of contents, ends with an index to scientific names, general index, and author addresses, and is well-organized. By-and-large, its multi-disciplined approach is an excellent introduction to the study of butterflies and fills a previous void with its publication.

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THE BUTTERFLIES OF EGYPT. Torben B. Larsen. 1990. Apollo Books, Lundbyvej 36, DK-5700 Svendborg, Denmark, 112 pp. (Available from the publisher for 240 Danish kroner + postage.)

Torben Larsen has systematically documented the butterfly fauna of much of the Near East, beginning with his classic *The Butterflies of Lebanon* (1974). This latest contribution presents the small fauna (58 species, fewer than recorded in most California counties) of a large, but very arid, country. Although the total documentation is much less than that available for some other regional faunas published by Larsen, he does a thorough and painstaking job as usual. The habitats and the butterflies themselves are illustrated in handsome and well-produced color plates. There are the usual Larsen treatments of biogeography, faunistics, migration and life-history strategies. The format is meant to match the Lebanon book.

At this writing, there are about 6.4 kroner to the dollar. This comes out to about $37.50, or 33c/page. In other words, this is not a cheap book. It will be indispensable for regional specialists, but something of a luxury for the average collector. For those interested in life-history evolution, adaptation to seasonality, or community composition, all of Larsen's work provides raw material for the study of functional convergence. This is no small contribution.

Arthur M. Shapiro, *Department of Zoology, University of California, Davis, CA 95616, USA.*

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Manuscript format: Two copies *must* be submitted, double-spaced, typed, with wide margins. Number all pages consecutively. If possible italicize rather than underline scientific names and emphasized words. Footnotes are discouraged. Do not hyphenate words at the right margin. All **measurements** must be metric. **Time** must be cited on a 24-hour basis, standard time. Abbreviations must follow common usage. **Dates** should be cited as: day-Arabic numeral; month-Roman numeral; year-Arabic numeral (ex. 6.IV.1984). Numerals must be used for ten and greater e.g. nine butterflies, 12 moths.

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Title material: All papers must include the title, author's name, author's address, and any titular reference and institutional approval reference. A **family citation must** be given in parenthesis (Lepidoptera: Hesperiidae) for referencing.

Abstracts and Short Papers: All papers exceeding three typed pages must be accompanied by an abstract of no more than 300 words. Neither an additional summary nor key words are required.

Name citations and Systematic Works: The first mention of any organism should include the full scientific name with unabbreviated author and year of description. There **must** be conformity to the current International Code of Zoological Nomenclature. We strongly urge depositing of types in major museums, all type depositories must be cited.

References: All citations in the text must be alphabetically listed under Literature Cited in the format given in recent issues. Abbreviations must conform to the *World List of Scientific Periodicals*. Do not underline or italicize periodicals. If four or less references are cited, please cite in body of text not in Literature Cited. For multiple citations by the same author(s), use six hyphens rather than repeating the author's name.

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Cover Illustration: Collage of *Philotes sonorensis sonorensis* in flight. From cover illustration of R. Mattoni, *Butterflies of Greater Los Angeles*, 1990. Original photograph by Greg Ballmer.